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The phylogeny of the Angiosperms

DOUGLAS HOUGHTON CAMPBELL

(WITH THREE TEXT FIGURES)

It is superfluous to state that the origin and interrelationships of the Angiosperms present problems whose final solution, if ever attained, must lie in the distant future. Nevertheless it may be worth while to examine the most recent contributions to the subject[1]—as some of these are of great importance—, and to compare the very divergent theories offered to explain the origin of the Angiosperms and their subsequent evolution.

Of course it is clear that any attempt to explain the ancestry of the Angiosperms is necessarily largely hypothetical and involves the much disputed question as to whether they are strictly monophyletic, or whether there are several independent phyla, or at any rate separate lines of descent extending further back than any record at present available.

There is an increasing tendency to assume a polyphyletic origin for the Angiosperms, and it seems much more likely that the 'family tree' will prove to be a much branched shrub, with sundry outlying suckers spreading from its roots. The very interesting discovery (Thomas, 27) in the Jurassic, of fructifications which may be called angiospermous, but which differ radically from any known Angiosperms, either recent or fossil, suggests that some of the existing phyla may also have had a quite independent origin.

The assumption of some ideal floral type from which all others have been derived still has its advocates, but it is likely that most students of floral evolution will be inclined to look for a polyphyletic origin for the larger groups of Angiosperms. This conclusion seems justified both from a morphological study of living types, and from the geological evidence.

It is true that the geological record is still very incomplete; but with the discovery of new fossil types, and a more thorough investigation of material already at hand, very substantial

[1] Hutchinson (12); Wettstein (28); Engler (9).

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progress is being made in the history of fossil Angiosperms.

The most recent advocate of the monophyletic origin of the Angiosperms is Mr. J. Hutchinson (12), Assistant at the Kew Herbarium. He aims to present a new classification of the Dicotyledons, based on phylogeny. He defends the Bentham and Hooker system as more nearly representing genetical relationships than does the system of Engler, which is now in general use in the United States. However, he has to admit very obvious defects in the former system.

Hutchinson assumes that the primitive angiospermous flower was bisporangiate, apocarpous, and with a petaloideous perianth—a type closely resembling the existing Magnoliaceae and Ranunculaceae— and from such a floral type he would derive all others. The apetalous and diclinous orders are supposed to be reduced from petaloideous and bisporangiate ancestors. Thus the orders considered as most primitive in the Engler classification are, according to Hutchinson's view, the ends of series originating with the Magnoliales and Ranales.

Diverging at a very early period, Hutchinson recognizes two great series of Dicotyledons. One of these is made up principally of trees and shrubs, and is traced back to the Magnoliales; the second series, predominantly herbaceous, begins with the Ranales. Where, as in the Compositae and Umbelliflorae, both woody and herbaceous genera are found, Hutchinson reaches the remarkable conclusion that these have arisen quite independently in the two great series; i.e., there exist within a single order, as generally recognized, genera which are not genetically related, but have developed independently as the end members of two widely separated lines of evolution. It hardly seems likely that this conclusion will be accepted without much more evidence than at present is offered by Mr. Hutchinson.

The interrelationships of the 76 orders of Dicotyledons recognized by Hutchinson are graphically shown in a very ingenious diagram. While many of these relationships will be accepted readily by most taxonomists, it is very doubtful whether they will be equally ready to subscribe to some of the others.

Another well-known British botanist, Dr. A. B. Rendle (22) also has recently published a work covering much the same

ground as that of Hutchinson, but differs widely from him in regard to the classification of the Dicotyledons. With slight modifications Rendle adopts the classification of Engler in the *Natürlichen Pflanzenfamilien*. He makes some changes in terminology and in the sequence of the orders, some of which are subdivided; but the changes for the most part are of minor importance. He agrees with Engler in considering the apetalous orders—e.g, Salicales, Piperales, etc.—not only as the simplest, but as the most primitive, and not closely related to the petaloideous orders.

Hutchinson's views are influenced strongly by Arber's (1) interesting papers on the origin of Angiosperms, and also by the earlier work of Bessey (4), who, like Arber, assumes a monophyletic origin for the Angiosperms. Arber's papers were inspired by the remarkable discoveries of the 'flowers' of the fossil Bennettitales (Cycadeoideae), especially Wieland's (29, 30) brilliant investigations on the wonderfully preserved fructifications of these plants from the Mesozoic formations of the Black Hills in Wyoming and South Dakota.

Arber concluded that the Cycadeoids were more nearly related to Angiosperms than to the true Cycads, and that the 'flower' was really homologous with the flower ('anthostrobilus') of the primitive Angiosperms; but did not claim that the latter are directly descended from Cycadeoids, but that the two have developed from a common stock.

Arber's papers were published before the discovery of the remarkable Cycadeoids, *Williamsoniella* and *Wielandiella*,[2] which much more nearly approach, in the structure of the 'flower', the simpler Polycarpicae. Unlike the Cycadeoids of the lower Cretaceous, whose habit was much like that of the true Cycads, these forms had slender forking stems and small scattered leaves. Wieland (30) believes the Dicotyledons may have come from forms resembling these, and may have existed as far back as the Permian. He says:

> From the Carboniferous to the Cretaceous there is, then, a great and cosmopolitan Cycadeoid group, with simple, sparsely inserted leaves. This group is especially abundant in the Rhaetic, a period of marked change in plant alignment.

[2] Thomas (26), Pontonié (20).

Wieland holds that the development of numerous nearly parallel stocks is much more likely than a 'dichotomizing' common stock from comparatively recent ancestors. He also believes that many supposed homologous structures are really homoplastic.

Arber proposes the name 'Hemi-angiosperms' for an hypothetical group of Mesozoic plants from which all fossil and recent Angiosperms have been derived. The flower ('pro-anthostrobilus') was similar to that of the Cycadeoids, but not derived directly from it. The 'pro-anthostrobilus' (figure 1,*1*) is conceived as a strobilus subtended by several series of perianth leaves, above which were several series of microsporophylls

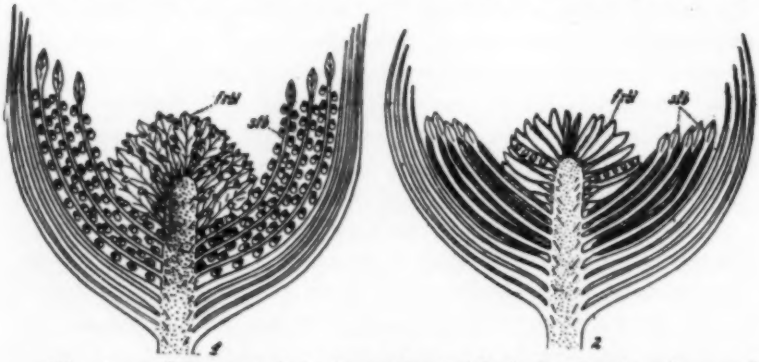

Fig. 1. *1*. Structure of the 'proanthostrobilus' of a 'hemi-angiosperm.' *2*. Flower (anthostrobilus) of a primitive Angiosperm—after Arber and Parkin.

with numerous synangia, and finally a terminal group of leaf-like 'carpels' with numerous marginal macrosporangia, these carpels being more reminiscent of the true Cycads than of the Cycadeoids.

It is clear that both Arber and Hutchinson subscribe to the long accepted dogma that all the floral organs are 'metamorphosed' leaves, a view hard to reconcile with what is now known as to the nature of the spore-bearing organs of the most ancient vascular plants.

Arber admits the great difficulties involved in passing from the hypothetical pro-anthostrobilus to the flower of the Ranalean type, from which he assumes all other floral structures have been derived. He believes the primitive Angiosperms were entomophilous and that entomophily was a very early and most

important factor in the origin of Angiosperms; indeed he thinks it may have originated with Hemi-angiosperms.

The assumption that the primitive Angiosperms had flowers of the Ranalean type, such as *Magnolia*, and that all other floral types are derivatives of this, is pure hypothesis, and based almost entirely upon a comparison of existing genera, largely ignoring the geological evidence, which is far from being in accord with such an hypothesis.

That Magnoliaceae did exist in the Cretaceous seems to be certain; but the earliest known Angiosperms, from the lower Cretaceous, are almost without exception apetalous genera, like *Populus* and *Ficus*, or Monochlamydeae with inconspicuous, and presumably wind-pollinated flowers. If we accept Hutchinson's conclusions that these early types are descended from a long line of petaloideous ancestors, we must believe that in the lower Cretaceous, and presumably in the Jurassic, there existed the petaloideous ancestors of these lower Cretaceous Apetalae. Since at present no traces of these alleged ancestral types are known (unless we accept the Cycadeoideae as such) either associated with the lower Cretaceous Angiosperms, or in earlier formations, it is fair to conclude that they did not exist.

While the geological record is admittedly very incomplete, there is no question of the existence of Angiosperms in the lower Cretaceous. The earliest of these in the United States are from the Patapsco formations of Maryland and Virginia. Of these Knowlton (13) says:

> These are not only the oldest unquestioned plants of this group (Angiosperms) known in North America but they have been found to be as old as, if not older than, any similar plants found elsewhere in the world.

Sixteen families are represented, all of which are either apetalous, or have insignificant, often diclinous flowers; in short, all of the oldest known Dicotyledons were almost certainly wind-pollinated.

That entomophilous flowers could hardly have existed before the Cretaceous is indicated by what is known of the insects of the Jurassic (Handlirsch, 11), where the highly specialized flower-haunting insects, like the bees and butterflies, seem to have been quite absent. All of the known early fossil insects

are very primitive in character, and there is little reason to believe that they were adapted to the pollination of flowers.

It is quite possible that casual visits of some of these primitive insects may have been the beginning of the entomophilous habit which has played such an outstanding rôle in the evolution of both Angiosperms and insects, and by the end of the Cretaceous, it is clear that entomophily was well established, although for some reason, the insects of the Cretaceous are less known than those of the Jurassic.

Wettstein (28) quotes from an interview he had with Handlirsch:

> From the Jurassic, Lepidoptera are known, but only forms with no proboscis, and which could not have been flower visitors. Diptera are abundant, but of types which either do not visit flowers, or only very exceptionally. None of the Jurassic Hymenoptera had the mouth parts adapted to sucking honey.

Considering what is known of the geological history of the Angiosperms it is hardly likely that Mr. Hutchinson will convert many botanists to his views.

In the introduction to the Angiosperms, in the new edition of the *Natürlichen Pflanzenfamilien*, Engler (9) has treated at some length the question of the origin of the Angiosperms. He does not accept Hutchinson's hypothesis of the derivation from Cycadeoideae, nor Wettstein's theory of a direct derivation from forms related to the existing Gnetales. He therefore feels it necessary to assume the existence during the Mesozoic of an extensive complex of forms having many of the characters of the living Angiosperms, from which the latter have been derived. To this hypothetical group he gives the name Protangiosperms.

From the Protangiosperms it is assumed that numerous independent lines of Angiosperms arose, some being Monocotyledons, others Dicotyledons. Engler thinks it very unlikely that any of the existing phyla are descended from any other existing forms, but the main groups, or phyla, of living Angiosperms are to be considered rather as parallel lines of evolution originating independently from Protangiosperms. He makes the very interesting suggestion that a change (mutation?) in a single individual among many millions, might very well appear in a similar, if not identical, form in other indi-

viduals, thus giving rise to different races which would have much in common, but could hardly be traced back to a common ancestral form.

During the Jurassic the floras of all parts of the world were remarkably similar, and it may be inferred that the ancestors of the Cretaceous and Tertiary Angiosperms, whatever they may have been, were also widespread, and from these arose various independent phyla.

There is evidence that during this period there was a more or less complete separation of the main land-masses of the northern and southern hemispheres, such as occurred during the Permian, and perhaps the marked differences between the existing boreal and austral floras may have begun at this time. Thus the pines, firs, spruces, and most of the amentiferous trees, are essentially boreal, while the Araucarias, Podocarps, Proteaceae and Myrtaceae belong mainly to the southern hemisphere. Such isolated orders as the Salicales and Fagales of the northern hemisphere, and the Proteales, equally characteristic of the southern hemisphere, might be cited.

Engler predicates for his Protangiosperms the following characters: Bisporangiate flowers, with rudimentary perianth, or none; anemophilous; microsporangium opening by means of an endothecium; megasporangium with or without an integument, either basal or marginal in position; female gametophyte of the typical 8-nucleate type, the egg-apparatus homologous with an archegonium; embryo either monocotyledonous or dicotyledonous; the sporophyte with either open or closed bundles.

The absence from Mesozoic strata of fossils which can be interpreted as Protangiosperms is explained both by the difficulty of identifying seeds and wood, which might be attributed to true Angiosperms, and the fact that a large number of Protangiosperms are believed to have been herbaceous plants which were poorly fitted to leave recognizable fossil remains. It is not believed that these herbaceous types have given rise to the woody Dicotyledons of the lower Cretaceous, but the latter are assumed to be descended from woody Protangiosperms.

Since the earliest known Angiosperms from the lower Cretaceous are clearly related to existing genera, and indeed

apparently in many cases actually belong to these, it is clear that there must have existed true Angiosperms in older formations; and Engler suggests that these may have originated in some, as yet, unexplored formations in the Tropics.

The primitive Monochlamydeae of the lower Cretaceous are not considered to be the direct ancestors of the Dialypetalae, but the latter are derived from other ancestral forms which were contemporaneous with the ancestral Monochlamydeae and Apetalae.

Engler admits the possibility that the diclinous condition in such orders as the Fagales and Salicales may be secondary, but does not believe they are reduced from petaloideous ancestors. He also thinks it possible that even in the Protangiosperms some forms may have had coherent carpels. Among existing Angiosperms he cites the Pandanales as closely approximating his hypothetical Protangiosperms.

The conclusion is reached that, while within certain phyla of the Angiosperms the relationships are unmistakable, and one might, in a sense, trace them back to a common ancestor, the attempt to decide from what ancient group the Angiosperms as a whole are descended, must remain for the present, at least, purely hypothetical. While the Cycadeoideae offer a tempting comparison with the flower of certain Angiosperms, the attempt to homologize the sporophylls of the Cycadeoids with the carpels and stamens of the Angiosperms presents such great difficulties as to make any real relationship extremely unlikely. Engler finally suggests that the Protangiosperms may have come from eusporangiate ferns, perhaps allied to the Ophioglossales. He calls attention to the vascular bundles of the latter which are very like those of the Angiosperms, both open and closed bundles being found in the order. One might also suggest that it would be much easier to derive the stamens of the Angiosperms from structures like the sporangiophores of the Ophioglossaceae than from the microsporophylls of the Cycadeoideae.

Wettstein (28) assumes a direct derivation of the Angiosperms from Gymnosperms, but instead of seeking a connection with the extinct Cycadeoideae, he sees in the Gnetales the nearest living relatives of the ancestors of the Dicotyledons. The flower of the Angiosperms is interpreted, not as a strobilus

(anthostrobilus) derived from the 'flower' of the Cycadeoids, but as an inflorescence, comparable to that of the living Gnetales, and Wettstein holds that the flower of the most primitive Dicotyledons corresponds to an inflorescence in which the individual flowers are coherent (fig. 2).

The peculiar order Verticillatae, comprising the single genus *Casuarina*, is held to be the most primitive of existing Dicotyledons, but is not related directly to any other order, and is assumed to have arisen independently from the Gnetales. However, from a similar type of inflorescence, might have been derived the floral type of the other more primitive Monochlamydeae. The perianth is homologous with the bracts sub-

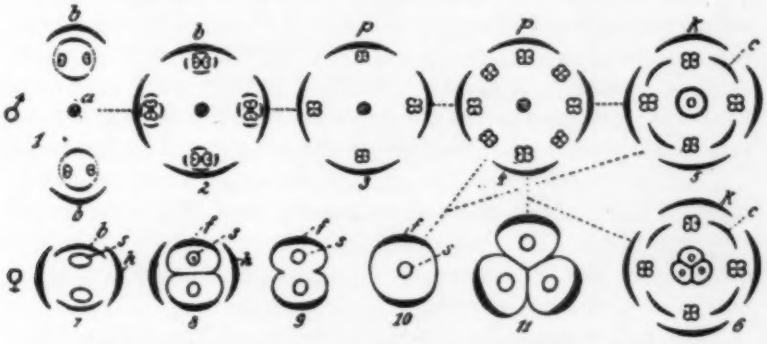

Fig. 2. Diagrammatic representation of the derivation of bisporangiate and dialypetalous flowers from a Gymnosperm inflorescence—after Wettstein.

tending the inflorescence, and opposite each is a single stamen. The next step in the evolution of the flower, according to Wettstein's theory, is an increase in the number of stamens. Later, some of the stamens became transformed into petals, this being associated with the development of the entomophilous habit.

The origin of the corolla from a transformation of stamens, rather than by a metamorphosis of perianth leaves, was first proposed by De Candolle, but this theory has not, perhaps, received from later writers the attention it deserves. While there are numerous examples of flowers in which the perianth is the showy part of the flower, as seen in many Monocotyledons, and in some Dicotyledons, in the Dialypetalae it is

much more likely that the corolla, at least, in most cases, is the result of a metamorphosis of the stamens.

Wettstein holds that the primitive angiospermous flower was monosporangiate, the perianth homologous with a circle of bracts, each subtending a single stamen, each stamen representing a reduced axillary flower, the four loculi of the anther in this typical flower resulting from the fusion of two bilocular stamens, such as occur in the staminate flower of *Ephedra*. In the megasporangiate flower the ovary is assumed to be formed by the union of two bracts, each subtending a single ovule, so that the primitive insertion of the ovules is basal, and not marginal.

The origin of the bisporangiate flower is explained by the occurrence of a megasporangial flower at the apex of a staminate inflorescence, so that there is a terminal ovary with the subtending stamens (staminate flowers). Wettstein maintains that this interpretation of the flower as an inflorescence is more easily understood than that which considers it to be a strobilus.

Wettstein points to the predominance of basal ovules in most Monochlamydeae as an indication that this is the primitive condition. He also points out the presence of vascular strands in the integuments of many Monochlamydeae, a condition common in many Gymnosperms.

The interrelationships of the 17 orders of Monochlamydeae recognized by Wettstein are very obscure. As already stated, the Verticillatae, which he holds to be the most primitive, are not related to any other order, and the same is true of the Proteales, which with the Santalales constitute an entirely independent phylum. Four other primitive orders, Garryales, Salicales, Batidales and Piperales, are isolated types of uncertain affinities. The remaining orders are more or less related to each other, and from some of these the higher types of Angiosperms have been derived.

Twelve orders of Dialypetalae are divided into two groups, one connected with the Monochlamydeae through the Hamamelidaceae, the other having its nearest relations among the Monochlamydeae in the Tricoccae. It is thus clear that Wettstein considers the Dialypetalae to have had a marked polyphyletic ancestry, and this is still more marked in the Sympetalae (fig. 3).

Whatever the ancestors of the Angiosperms may have been —true Gymnosperms, 'Protangiosperms', 'Hemi-angiosperms' —the weight of evidence is strongly in favor of the thories of

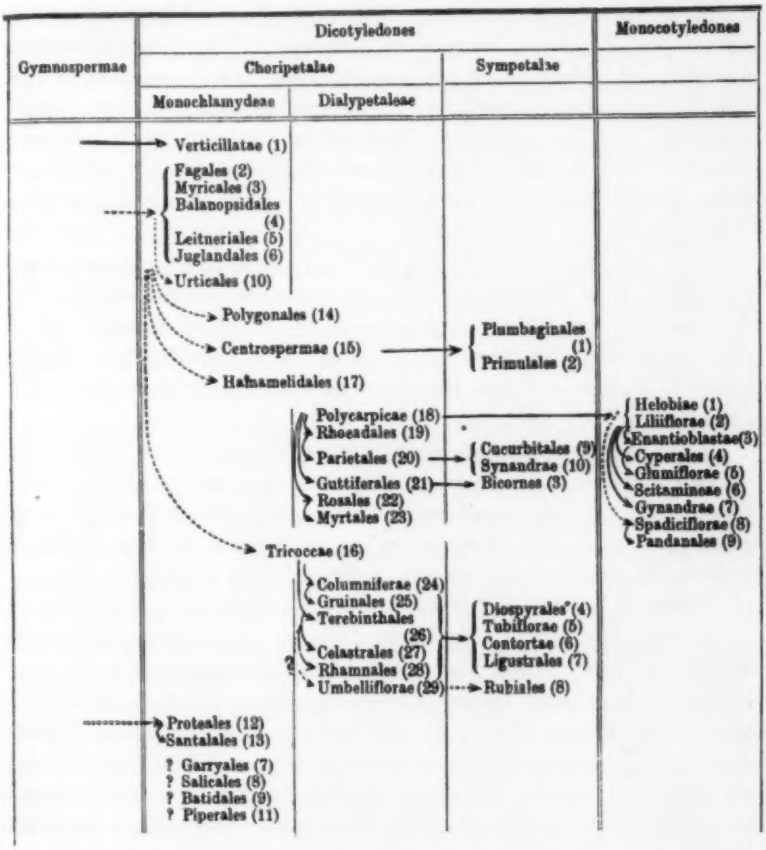

Fig. 3. Interrelationships of Angiosperms—after Wettstein.

Engler, Wettstein, and Wieland, that from a widespread and complex ancestral stock, many independent phyla of Angiosperms developed.

Hutchinson's assumption that the Polycarpicae are ancestral to all the other Angiosperms is purely hypothetical and based mainly upon a study of living forms, with scant reference

to the geological record, except so far as it concerns the Cycadeoids. If we accept this view, we must believe that the Polycarpicae existed far back of the Cretaceous, in order to account for the long series of intermediate forms between the Polycarpicae and the Monochlamydeae of the lower Cretaceous, the oldest Angiosperms known at present. The Cycadeoideae, upon which Arber based his speculations, are themselves of the lower Cretaceous, practically contemporaneous with true Angiosperms, and presumably themselves the end of a phylum derived from simpler types. Some of the latter, *e.g. Wielandiella*, as Wieland has held, certainly show some suggestive resemblances to Dicotyledons, but our knowledge of these is still too incomplete to decide how far these resemblances may indicate a true relationship. Until much more evidence for the existence of petaloideous Angiosperms in older formations is demonstrated, the predominance of Monochlamydeae in the lower Cretaceous floras justifies the conclusion that these are primitive rather than derivative types.

That the earliest Angiosperms were entomophilous is exceedingly doubtful. Aside from the character of the lower Cretaceous Dicotyledons, whose living relations have, for the most part, inconspicuous flowers, what is known of the Jurassic insects, as already pointed out, indicates that the highly specialized insects, such as butterflies and bees, had not yet come into existence, the very primitive Jurassic insects being types which, at best, could have served only accidentally in pollination. Just when entomophily became established, and thus started the extraordinary evolution of both insects and Angiosperms, it is impossible to state; but the rapid increase in the number and variety of Angiosperms in the later Cretaceous indicates that entomophily had begun to exercise a marked influence on their evolution, although very little is known of the insects themselves.

The development of a showy corolla is, of course, associated with the entomophilous habit, and it is by no means unlikely that the development of a true corolla was preceded by a condition in which the stamens, otherwise unchanged, became conspicuously colored, and thus attractive to insects. Such a condition still exists in a good many flowers belonging mostly to orders recognized as among the older, and probably more

primitive members of the Dicotyledons; *e.g. Thalictrum*, *Salix*, *Acacia* and other Mimoseae, *Eucalyptus*, *Callistemon*, and *Metrosideros* of the Myrtaceae. In these the corolla is either entirely wanting, or relatively inconspicuous. In this connection reference might also be made to the petaloid staminodia of *Mesembryanthemum* and *Canna*, and the transition from stamens to petals in the Nymphaeaceae. De Candolle, in assuming the origin of petals from the sterilization of sporophylls, rather than the origin of the latter from vegetative leaves, was decidedly ahead of his time.

If it is admitted that a number of independent phyla have arisen from the ancestral complex of the Jurassic, it is readily conceivable that one of these gave rise to the Ranalean series, while from another the primitive Monochlamydeae developed. While Engler is inclined to think that the diclinous Monochlamydeae may have had bisporangiate ancestors, Wettstein thinks it more likely that the monosporangiate floral type is more primitive than the bisporangiate, calling attention to the prevalence of the former among the Gymnosperms. The writer is inclined to agree with Wettstein in this respect.

In view of the discovery of a group of fossils in the Jurassic, which were truly angiospermous, but apparently quite unrelated to existing Angiosperms, it may be that other entirely independent Angiosperms may be discovered.

Engler's view that the typical 8-nucleate embryo-sac was characteristic of the Protangiosperms may be questioned. The most marked departures from the type occur principally among the more primitive orders, and although the 16-nucleate embryo-sac of *Peperomia* and *Gunnera* are regarded by Engler and some other writers as secondary rather than primitive, inasmuch as the embryo-sac is formed directly from the megaspore-mother cell, one may very well ask why, in these primitive genera there should be this marked deviation from the type, while in many other cases, *e.g. Lilium*, the embryo-sac has the normal 8-nucleate form, although, as in *Peperomia*, it is formed directly from the megaspore mother cell.

In any case, the argument cannot apply to *Pandanus* (Campbell, 6), where before fertilization the embryo-sac may contain upward of sixty nuclei, while the embryo-sac is formed from one of three cells resulting from the division of the mega-

spore mother-cell. This is especially significant, as Engler concludes that *Pandanus*, which has the most highly developed female gametophyte yet discovered in the Angiosperms—is very close to his hypothetical Protangiosperms.

It would seem quite as likely that these aberrant types of embryo-sac approach more nearly the condition in the ancestral Angiosperms than does the typical 8-nucleate embryo-sac.

It is quite conceivable that the primitive Angiosperms had a bi-polar embryo-sac and perhaps the typical egg-apparatus; but there was probably a greater development of the vegetative tissue (antipodal cells) of the gametophyte, such as occurs in *Pandanus*, before fertilization, and in *Sparganium* and a good many other Angiosperms, *e.g.* grasses, some Compositae, subsequent to fertilization.

Among the Gymnosperms the nearest approach to this condition is found in *Gnetum*, although the differences are too great to assume any near relationships. At any rate Wettstein's theory of a direct relationship between Gnetales and Angiosperms is consistent with what is known of the history of the embryo-sac.

The phylogeny of the Angiosperms has been treated recently from quite a new point of view, viz. the ecological conditions involved. Dr. J. W. Bews (5) has studied the ecological factors in South Africa, a very ancient region geologically, where presumably climatic conditions have remained relatively unchanged for a very long time. He concludes that the conditions existing when the first Angiosperms appeared were much like those of the moist tropics of today and that the tropical forests contain a larger percentage of primitive genera than the temperate regions, the types characteristic of the latter having first arisen as a result of cooler and dryer conditions resulting from the uplift of mountain ranges, and the adaptation of lowland plants to these new conditions. This theory is entirely in harmony with the evidences of geological climates during the Jurassic and Cretaceous, where it is evident from the similarity of the vegetation everywhere, that a very uniform and presumably warm climate prevailed over nearly the whole world.

In this connection, Coulter and Chamberlain (7) point out that the Monocotyledons for the most part are mainly tropical

in their distribution, the boreal types being relatively few. The predominance of aquatic types among the lower Monocotyledons is also quite in harmony with the theory of Bews, who thinks these aquatic forms were a feature of the early angiospermous floras.

The relative antiquity of Monocotyledons and Dicotyledons has been the subject of much controversy. While the majority of recent writers on the subject have been inclined to the view that the Dicotyledons are the older, and the Monocotyledons an offshoot from a dicotyledonous stock, this is not universally accepted. The geological record, so far as it goes, indicates that the Monocotyledons are about as old as Dicotyledons, but remains of the former are much less abundant, due no doubt, in part, to their predominantly herabaceous habit. As among Dicotyledons, the genera usually accepted as primitive, *e.g. Sparganium*, *Potomogeton*, palms, seem to be older than the petaloideous types.

The recent discovery (Noé, 18) of Carboniferous fossils having stems with a typical monocotyledonous structure, is decidedly interesting. Should these prove to be true Monocotyledons, it would be evident that the group is a very ancient one.

It is hardly likely that the differences in the embryo of the Monocotyledons and Dicotyledons are as fundamental as is generally taken for granted, and the polyphyletic character of the Monocotyledons is, at any rate, a possibility.

Aside from the embryo, there are no criteria by which we can absolutely separate the two primary divisions of the Angiosperms. No doubt some of the resemblances are due to homoplastic developments, but it is worth noting that among the lower members of both series are encountered numerous resemblances pointing to a real relationship. The case of the marked similarities existing between the Helobiales and Ranales, is sufficiently familiar, but it is surprising to find how many of the lower orders of the Dicotyledons show monocotyledonous characters. This is especially noticeable in the flowers which have the characteristic trimerous arrangement instead of the pentamerous one, so common in the Dicotyledons. Examples of this are the Aristolochiaceae, Berberidaceae, Lauraceae, Polygonaceae, Nymphaeaceae, Magnoliaceae, Ano-

naceae, Celastraceae. This might suggest that the trimerous flower, typical of Monocotyledons, may be an older type than the pentamerous flowers of the majority of Dicotyledons.

On the other hand, the reticulate venation, typical of Dicotyledons, has a good many examples among Monocotyledons, *e.g. Trillium*, *Lilium giganteum*, many Araceae.

The possibility of a direct connection of the Monocotyledons with Pteridophytes has been made (Coulter and Chamberlain, 7), suggested especially by the similarity to the Monocotyledons in the structure of both embryo and adult sporophyte in *Isoetes*. While *Isoetes* is perhaps most commonly associated with the Lycopodineae, it is much more likely that its nearest existing relatives are the eusporangiate ferns, which Engler also suggests may have given rise to the Protangiosperms.

Miss Sargant (23), from a very careful comparison of embryos of Monocotyledons, concluded that the monocotyledonous condition is secondary, and derived from the fusion of two cotyledons. This condition is often associated with a geophilous habit, where from a permanent subterranean axis, herbaceous shoots are developed. This condition is assumed to be secondary.

If, however, the possibility of a direct derivation of Monocotyledons from Pteridophytes is admitted, the geophilous habit might really be primitive, as most ferns are geophilous. The aquatic habit too, so common among Monocotyledons, might also be inherited from some heterosporous fern ancestors, as all the existing heterosporous Filicineae are either aquatic or amphibious. It might also be added, that the megaphyllous habit of so many Monocotyledons, e.g. palms, Araceae, Musaceae, might also be a remote inheritance from filicinean ancestors and not a secondary development from some microphyllous Dicotyledons.

CONCLUSION

Comparing the very divergent theories as to the origin of the existing Angiosperms, the weight of evidence appears to favor the views of Engler and Wettstein as to their polyphyletic character. Both comparactive morphology and the geological record indicate that the existing Angiosperms represent a number of distinct phyla which cannot be traced back to a

single ancestral type. The theory defended by Hutchinson, that all the Angiosperms have been derived from a single floral type, closely approximating that of *Magnolia* or *Ranunculus*, is not based upon very convincing evidence. The occurrence of such highly organized entomophilous flowers in the lower Cretaceous, not to mention the Jurassic, is highly improbable.

The attempts to connect these floral types with the fossil Cycadeoids are not very satisfactory, especially when the very great differences between the sporophylls of the Cycadeoids, and the carpels and stamens of the Angiosperms are considered.

As to the hypothetical Mesozoic ancestors of the Angiosperms, Arber's 'Hemi-angiosperms,' and Engler's 'Protangiosperms,' the latter are more plausible, as Engler assumes for them sufficient range of structure to allow for the development of many independent phyla of true Angiosperms.

Comparing the two hypotheses concerned with the morphology of the flower of the Angiosperms, viz. whether it is a strobilus, as Arber and Engler believe, or an inflorescence, as interpreted by Wettstein, it must be admitted that there is evidence for both, so it is possible that both may be true. Certainly Wettstein's explanation of the flower of the lower Dicotyledons, especially the origin of bisporangiate flowers, is easier to understand, on the assumption that the flower corresponds to a reduced inflorescence, rather than to a simple strobilus. It also seems to the writer that Wettstein's assumption that the monosporangiate flower is primitive is more probable than that it is reduced from a bisporangiate flower.

That the ancestral Angiosperms had a more highly developed female gametophyte than the typical 8-nucleate embryo sac is indicated by the increase in the number of nuclei found in some of the simpler and presumably older genera. The most noticable case is the very greatly increased number of nuclei in the embryo-sac of *Pandanus*.

While the Monocotyledons are much more uniform in structure than the Dicotyledons, it is probable that they also represent more than one phylum derived perhaps from the 'Protangiosperms,' but not from Dicotyledons.

The possibility of a direct derivation of the Angiosperms from Pteridophytes (Engler suggests the eusporangiate ferns) is at any rate worth considering. As the Monocotyledons more

nearly resemble the ferns in their structure, than do the Dicotyledons, this theory would point to their being the older type. The recent discovery of Carboniferous fossils, claimed to be Monocotyledons, may also indicate the latter to be older than the Dicotyledons.

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A morphological and cytological study of Ipomoea trifida

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(WITH THIRTEEN TEXT FIGURES AND PLATE 14)

The family Convolvulaceae has received very little attention from the morphologist and cytologist. Aside from the work of Kayser (7), Peters (11), and MacPherson (9), references to the group have been largely incidental.

Kayser (7) noted in *Ipomoea purpurea* a massive growth of the integument, producing a very long micropylar canal. The nucellus is very small, and is absorbed early by the developing embryo sac.

The present writer has been unable to obtain Peters' work 'Vergleichende Untersuchungen ueber die Ausbildung der sexuellen Reproduktionsorgane bei *Convolvulus* and *Cuscuta*,' a dissertion from Zurich which was evidently published privately. Suchürhoff (13) states, on the authority of this work of Peters, that the two genera mentioned in his title form hypodermal archesporial cells, which become deeper lying through the cutting off of parietal cells. No definite statement seems to have been made with respect to the structure of the embryo sac. Dahlgren (4) regards Peters' evidence of the presence of parietal tissue as unsatisfactory. Certain figures from Peters are cited in which the embryo sac mother cell and spore tetrads are represented in contact with the epidermis. Others, which seem to show parietal tissue, are explained as not being cut parallel with the long axis of the nucellus. Dahlgren presents an illustration from his own material of a nucellus of *Cuscuta lupuliformis* with an embryo sac mother cell in synapsis, lying in contact with the epidermis. He also cites a case of an embryo sac in contact with the epidermis in *Cuscuta Epithymum*. He regards parietal cells in the Sympetalae proved with certainty only in the Plumbaginaceae and the Cucurbitaceae.

Asplund (1) working on *Convolvulus lupuliformis*, confirms Peters' view as to the hypodermal origin of the archesporial cells. Svensson (15) is of the opinion that the archesporial cells shown by Peters are indirectly of epidermal origin.

Miss MacPherson (9) in her work on *Convolvulus sepium* and *Cuscuta Gronovii*, does not show any stages earlier than the

binucleate embryo sac. It is, therefore, impossible to determine the origin of the peculiarly shaped embryo sac in the species studied by her, or to trace the development of the tissues of the ovule so as to be sure just what tissues remain at this stage of development. She states that in *Convolvulus sepium* polyembryony is the usual course of development, and that the multiple embryos seem to have developed from the synergids. Large vacuolate suspensors are typical of the older embryos in *Convolvulus sepium*, but no suspensors were found in *Cuscuta*. She shows a long, narrow, curved embryo sac in both *Convolvulus sepium* and *Cuscuta Gronovii*, the former differing strikingly from the latter in that the antipodal cells migrate to the micropylar end of the sac along with the egg apparatus and polar nuclei. According to her study, the nucellus of both species is very large, and persists so that it surrounds the mature embryo sac.

Coulter and Chamberlain (2) state that the endosperm of *Cuscuta* is scanty and is formed by free nuclear division, contrary to the usual development of endosperm in parasites; and, that the embryo also is an exception in the morphology of parasites, in that it is large and well developed. These points were confirmed several years later by MacPherson (9) in the above mentioned work on *Cuscuta Gronovii*. Dahlgren (3) reports endosperm formation by free nuclear division in *Convolvulus lupuliformis* and also in *Pharbitis purpurea*.

Many systematic botanists place *Cuscuta* in a family by itself, excluding it altogether from the Morning Glory family (Small, Britton, and others). Yuncker (17) in his recent revision of the genus *Cuscuta*, accepts the old view held by Englemann and Gray, and includes *Cuscuta* as a sub-group of the Convolvulaceae.

In this report on the morphology of *Ipomoea trifida* G. Don var. *Torreyana* Gray, special attention has been given to the origin of the long, narrow, curved embryo sac, and to the growth of the latter into the micropyle so that it is the integument and not the nucellus that immediately surrounds the embryo sac.

Part of the material for this study was collected in October and November, 1926. It was necessary to supplement this collection in the spring of 1927 in order to secure all of the desired

stages of development. All of the material was obtained from neglected spots on the University of Texas campus.

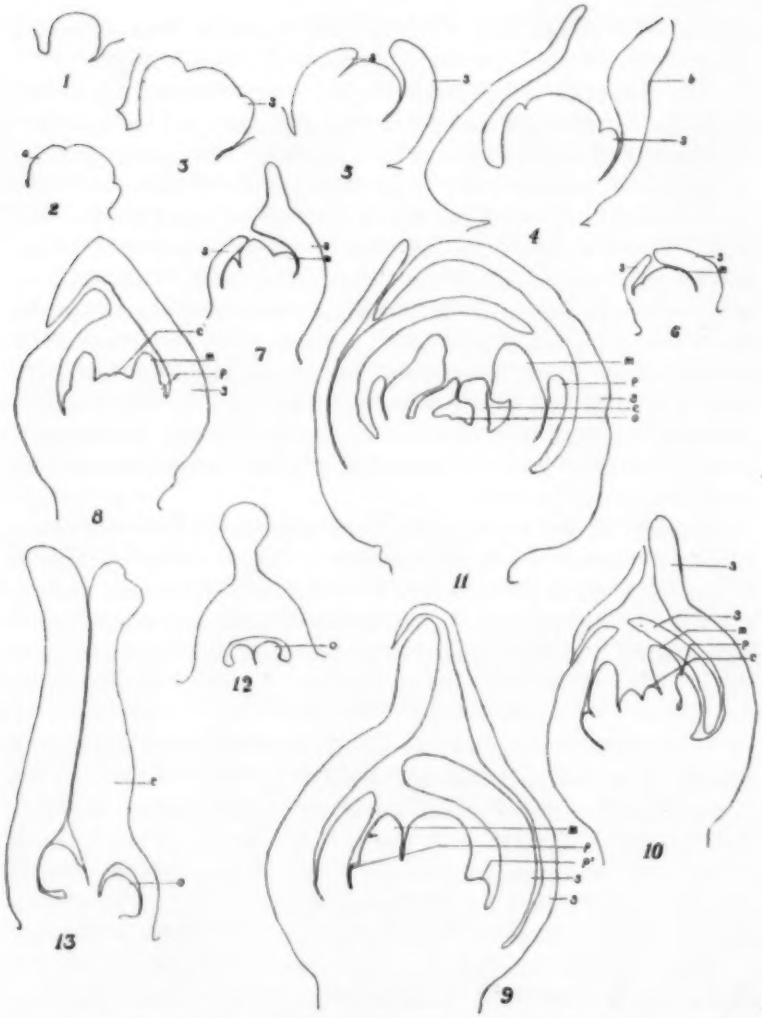
The material of different stages of development was collected at convenient hours during the day and fixed immediately in different fixatives. Flemming's medium, Flemming's strong, strong chromo-acetic, and weak chromo-acetic were used. The very young buds were placed intact in the fixing fluid. The sepals were removed from older buds, while the oldest buds and flowers were dissected and only the pistils fixed. This not only securred better penetration, but made sectioning easier, for the floral parts harden during the processes of fixation and infiltration. Very young seeds were fixed in the capsules; but, with older capsules, the seeds were dissected out before fixation. Perhaps the best results were obtained from the Flemming's strong fixative. Some of the young buds were dissected and studied without fixation.

Sections of the young and of the older buds were cut seven and ten microns thick respectively. These were stained in Flemming's triple stain and in Heidenhain's iron-alum haematoxylin. Flemming's stain gave the best results for the morphological work and Heidenhain's for the cytological.

FLORAL DEVELOPMENT

In the early years of the study of floral development it seemed to be assumed that in the majority of cyclic flowers, the cycles appeared in acropetal order; e.g., sepals, petals, stamens and carpels. In later years it has been found that the exceptions to this order of succession are numerous. Hofmeister (6) records that in *Rosa*, *Potentilla* and *Rubus* the primordia of the carpels appear before those of the stamens have reached the full number, and that in *Hypericum calycinum* the primordia of the sepals appear after those of the stamens. Coulter and Chamberlain (2) call attention to the fact that among the Compositae, Dipsacaceae, Valerianaceae and Rubiaceae, in which the sepals are much reduced or modified, their primordia do not appear until after those of the stamens and carpels; and that among the Cruciferae the petals are the last members to appear.

Pfeffer (12) noted in the flower of the Primulaceae that the petals appear after the stamens, and each apparently from the dorsal surface of a young stamen. Coulter and Chamberlain



Figs. 1–13. Floral development of *Ipomoea trifida*. Drawings made by the aid of the camera lucida, and reduced in reproduction to the magnifications indicated. Letters used to designate the parts of the flower: *s*, sepal; *m*, stamen; *c*, carpel; *p*, petal or coralla lobe; *o*, ovule; *b*, bract.

Fig. 1. The primordium of a flower bud, a knob-like projection of undifferentiated tissue. ×40. Figs. 2, 3. The sepals appearing as lateral lobes. ×16.8. Fig. 4. A terminal bud showing two large protective bracts or bud scales, and sepals appearing as lobes on the side of the bud. ×40. Fig. 5. The sepals enclosing the bud. ×40. Figs. 6, 7. The stamens appearing as a second

(2) are of the opinion that in this case the primordia of the stamens and petals have a common origin.

In *Ipomoea trifida* the cycles of floral parts appear in the following order: sepals, stamens, carpels, and petals (text figs. 2–11). The primordia of the flower buds appear in the axils of the leaves, or as terminal buds, and are protected by scales or bracts. The buds appear at first as small knob-like projections of undifferentiated tissue (text fig. 1). Then the sepals appear as lateral lobes of this undifferentiated tissue (text figs. 2–5), and gradually enclose the young bud. The stamens follow next, forming a second series of lobes, somewhat larger than the first (text figs. 6, 7). At first they grow upward (text figs. 8, 9, 10), then as the anthers are differentiated and become greatly enlarged, the stamens bend in towards the center (text fig. 11). The primordia of the two carpels and of the petals seem to appear at nearly the same time. The former appear from the center of the bud just within the cycle of stamens (text figs. 8, 10, 11), and the latter appear just outside the cycle of the stamens and alternate with them. In dissections of very small buds, five distinct, unconnected corolla lobes may be observed. Although they alternate with the stamens the latter form such a crowded cycle at this period that the corolla lobes very early overlap their bases and are seen to be fused with them at the points of contact. At a slightly later stage a continuous zone or tube is formed beneath the five corolla lobes and they are carried upward on this tube. In the mature flower the stamens are attached to the gamopetalous corolla for a distance of 8–10 mm. Before the carpels have fused, forming the style and

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series of lobes within the protective sepals. ×40. Fig. 8. Section of a bud showing the sepals enclosing the bud; the large stamens with anthers not yet differentiated; the carpels arising at the center; the primordia of the petals overlapping the base of the stamens. ×40. Fig. 9. Section of a bud showing overlapping sepals and large stamens. *p*, section of petal at point of attachment to stamen; and *p'*, section of petal between the stamens. ×20. Fig. 10. Section of young bud with overlapping sepals, the anthers beginning to differentiate at the top of the stamens. ×40. Fig. 11. Section of an older flower bud, showing all the cycles of floral parts. ×48. Fig. 12. Section through the edge of the pistil showing the two ovules of one cavity. ×16. Fig. 13. Section of an older pistil showing incomplete fusion of carpels, the two ovarial chambers and only one of the ovules of each chamber. ×20.

ovarial chambers, the primordia of the ovules may be seen slightly elevated above the floor of the cavity (text fig. 11).

A two-chambered ovary is formed by the fusion of the two above mentioned carpels (text fig. 11). Normally, there are two ovules in each cavity (text fig. 12). The primordia of the ovules appear as small knob-like projections from the placenta at the base of the ovary. For a short time they grow upward, forming short knobs (text fig. 12). Then they take a transverse course across the cavity, and begin to bend slightly downward (text fig. 13). The nucellus and integument have begun to differentiate by the time that the opposite wall of the cavity is reached. The nucellus appears first, projecting at an angle of about 45 degrees to the vertical axis of the cavity (pl. 14, figs. 1, 2, 3). It has, at this early age, a well defined epidermal layer. The cells of the nucellus are rich in cytoplasm and have very large nuclei. The rudiments of the integument appear soon after, and gradually enclose the nucellus (pl. 14, figs. 4a, 4b, 5). As growth proceeds, the longitudinal axis of the nucellus is directed towards the floor of the ovary; and, by the time that this tissue is enclosed by the integument, the complete anatropous condition is reached.

The integument continues its growth, becoming very massive and extending far beyond the nucellus. Growth is very much more rapid in that part of the integument extending beyond the nucellus, and in the region of the funiculus. Consequently, the nucellus is pushed higher and higher in the ovarial chamber. By the time that the entire cavity is filled, the nucellus is well in the chalazal end of the ovule. The micropyle, therefore, has undergone extreme elongation, and, at this stage, extends from two-thirds to three-fourths the length of the ovule. The side of the integument towards the outside wall of the cavity grows faster than the other side. This causes the ovule to curve inward so that the mouth of the extremely curved micropyle of the mature ovule is in contact with the funiculus (pl. 14, figs. 13b, 16b).

Even before the primordium of the integument has appeared, one or more cells, entirely unlike the other cells, are to be seen in the young nucellus. These cells are somewhat larger than the other nucellar cells, and are always easily recognized by the unusually large nuclei and very large, deeply stained

nucleoli. None of the other cells of the nucellus contain such large nuclei, nor such conspicuous nucleoli. The number of these large cells varies from one to four (pl. 14, figs. 1, 2, 3, 4a). A greater number of the ovules contain two (pl. 14, figs. 1, 2). They usually lie in a row parallel to the longer axis of the nucellus (pl. 14, figs. 1, 2) though this is not always the case. Not infrequently two of the cells are to be seen lying in a plane approximately at right angles to the long axis of the nucellus. Four such cells have been observed lying roughly tetrahedrally near the center of the young nucellus (pl. 14, fig. 3). Although these cells lie touching one another they do not always lie in such a position as to lead one to the belief that they have arisen from a common cell. In part of the cases observed, they have undoubtedly arisen independently. Frequently the outer one lies in contact with the epidermis (pl. 14, fig. 2) though this is not always the case, for, as will be seen in plate 14, figure 1, it may lie embedded, at least one cell below the epidermis. From the position of these cells and their state of differentiation, they are probably to be regarded as archesporial cells.

This condition of multiple archesporial cells in the very young nucelli, may lead one to suspect that they give rise to multiple megaspore mother cells. But, as the ovule enlarges, only one of these conspicuous cells functions. This one grows more rapidly than the others. The sterile cells of the nucellar tissue undergo enlargement, also, and become like the non-functioning archesporial cells in size and nuclear characteristics. The latter can then no longer be distinguished from the surrounding nucellar cells.

Whether any of the archesporial cells divide after they are differentiated, the author is unable to say. From a study of the position of the mother cells in the older nucelli, it seems very probable that any one of the archesporial cells may function. Apparently, the innermost one develops usually, for the mother cell is more often found deeply embedded in the nucellar tissue (pl. 14, figs. 6, 8). This is not always the case, however. Plate 14, figure 4a shows the mother cell separated from the epidermis by only one layer of cells. The mother cell in synapsis in plate 14, figure 7a lies just under the epidermis. The epidermis is nearly disintegrated, and it is not improbable that other cells within the epidermis have also undergone disintegration.

The megaspore mother cell enlarges and its nucleus enters synapsis. At this stage, the nucellus is completely enclosed by the integument. At the time of the recovery from synapsis, the integument has grown to such an extent that the micropyle is more than half the length of the ovule. The nucellus is left well in the upper half of the ovule.

A linear series of four megaspores is formed (pl. 14, fig. 10), and the innermost cell develops into the embryo sac (pl. 14, fig. 11a). As the functioning megaspore grows larger, the other megaspores, together with the remaining nucellar tissue, are absorbed (pl. 14, fig. 11a). In some cases the nucellus is practically consumed before megasporogenesis (pl. 14, fig. 7a).

The eight-nucleate embryo sac is formed, in the usual manner, by three successive divisions of the functioning megaspore. About the time of the second division of the megaspore, the embryo sac, having consumed the remainder of the nucellus, begins to grow out into the micropyle, absorbing the inner layers of the integument as it proceeds (pl. 14, fig. 13b). At first, when the embryo sac is small, the micropylar canal seems to be large enough to accommodate it, and very little of the adjacent integument tissue is absorbed. The sac conforms to the size, as well as the shape, of the long, narrow micropyle. The growth of the sac through the upper end of the micropyle is apparently very rapid. By the time of the third division of the megaspore, the embryo sac is four times as long as it was at the time of the second division. At the time of the last division, the lower end of the sac has progressed far towards the outer end of the micropyle. At this stage, the sac is very long and narrow, and decidedly curved (pl. 14, fig. 14). The nuclei extend from one end of the sac to the other, and tend to be in pairs which are obviously sister nuclei. The protoplasm is aggregated about the pairs of nuclei, and large vacuoles appear between the groups. As the embryo sac enlarges, the nuclei undergo a rearrangement. The small antipodal nuclei are pushed to the extreme upper end of the sac by the enlargement of the vacuole below them. The polar nuclei become large and prominent. The nuclei of the egg apparatus, together with the polar nuclei, and large quantities of protoplasm, migrate to the lower end of the sac.

The organization of the membranes about the nuclei of the

egg apparatus and antipodal cells does not take place until the sac has elongated to such an extent that the egg apparatus lies only a very short distance from the mouth of the micropyle (pl. 14, figs. 16a, 16b). The sac is broader at the micropylar end and is extremely curved. The synergids and egg are pear-shaped. The polar nuclei take a position near the egg apparatus, but do not fuse until after fertilization. The antipodal cells begin to degenerate in the upper end of the sac immediately after formation. They have disappeared entirely considerably before fertilization. The synergids disappear just before or about the time of fertilization. Double fertilization was observed. One male nucleus was seen lying in contact with the nucleus of the egg, while the other had begun to fuse with the polar nuclei.

The author has not been successful in obtaining a sufficient series of embryos to warrant any statement in regard to the development of the embryo or the condition of polyembryony in *Ipomoea trifida*.

DISCUSSION

The floral development of *Ipomoea trifida* is similar to that which Pfeffer (12) found in the Primulaceae, in that the petals develop after the stamens and before, or simultaneously with the carpels. The corolla tube is attached to the bases of the stamens from the time of its first appearance.

The usual criteria for distinguishing archesporial cells from other cells in the nucellus seem to be conspicuous size of the cells, contents which stain differently from the other cells, and often conspicuous nuclei. At times, however, when there are no such conspicuous cells, position in the nucellus has been used as a means of identification.

It is quite probable that the origin of the archesporial cells varies in different species, the cells arising in some cases from a definite region in the tip of the nucellus, and in other cases arising from any of the cells in the apex of the nucellus, any or all of these cells being potentially archesporial. *Ipomoea trifida* seems to belong to this latter class. Cells of conspicuous size and with very conspicuous nuclei and nucleoli are to be seen in various positions in the young nucellus. Although the number of such cells varies from one to four, only one has been observed to function as a mother cell.

The author can not say with certainty whether the archesporial cells ever divide after they are differentiated. It seems quite possible that the archesporial cell functions directly as the mother cell.

A linear series of four megaspores is formed, the chalazal one developing into the embryo sac. The functioning megaspore consumes the remaining nucellar tissue, and by the time of the second division of the megaspore, the young embryo sac begins to grow out into the long, curved micropyle. Some of the cells of the inner layers of the integument are consumed as the embryo sac moves forward towards the outer end of the micropylar canal. It conforms to the shape of the long, curved micropyle. At the time of the organization of the egg apparatus and antipodal cells, the lower end of the long, curved embryo sac is only a very short distance from the mouth of the micropyle.

The long, narrow, curved embryo sac observed in this study appears to be typical of the Convolvulaceae. At least, it has been observed in the three species, *Cuscuta Gronovii*, *Convolvulus sepium*, and *Ipomoea trifida*. Though Miss MacPherson does not report early stages in the development of the ovule in her work on *Cuscuta Gronovii* and *Convolvulus sepium*, it seems quite possible that the nucellus is absorbed and that the embryo sac grows into the micropyle, in both forms, as in *Ipomoea trifida*. This condition is not characteristic of the Convolvulaceae alone; but it has been reported in many other groups. Weinstein (16) in a recent paper on *Phaseolus vulgaris* states that the micropylar end of the nucellus is consumed by the embryo sac, except the capping cells that persist as a hood over the end of the sac until an advanced stage in the development of the embryo is reached. The embryo sac grows into the micropyle, pushing the cap on ahead of it.

Lloyd (8) reported that the embryo sac in Galieae and *Diodia* of the Rubiaceae breaks through the capping cells of the nucellus and passes down the micropyle. Ferraris (5) states that in *Hemerocallis*, *Crocus*, *Gladiolus*, and *Romulea* the nucellus is used up, and that the embryo sac protrudes, more or less, into the micropyle. This condition was also reported by Murbeck (10) in *Alchemilla;* and by Strasburger (14) in *Medicago* and *Torenia asiatica;* by Lloyd (8) in the Labiatae and in *Vaillantia*. In *Vaillantia* the mother cell migrates into the

micropyle and develops there. In *Torenia* (Strasburger,14) the form in which we find the oldest and most conspicuous illustration of this phenomenon, the embryo sac passes beyond the micropyle and even reaches the ovary wall.

SUMMARY

1. In *Ipomoea trifida* the petals develop after the stamens. The corolla becomes tubular by the formation of a continuous zone or tube below the rudimentary petals.

2. Although one to four cells, conspicuous in size and nuclear characters, may be differentiated in the young nucellus, only one has been found to function as a mother cell.

3. The mature integument extends far beyond the nucellus, forming a very long micropyle.

4. The developing embryo sac consumes all of the nucellar tissue and grows out into the long, narrow, curved micropyle.

This study was undertaken at the suggestion and under the direction of Professor Frederick McAllister. The writer wishes to thank Professor McAllister for his encouragement and invaluable assistance throughout the course of the investigation.

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Explanation of plate 14

All drawings were made with the aid of the camera lucida, and have been reduced a little more than one-half in reproduction, with the result of approximate magnifications indicated after each figure.

Fig. 1. Section of a very young nucellus, showing two sub-epidermal cells, conspicuous in size and nuclear characteristics. ×192.

Fig. 2. Two conspicuous cells in a young nucellus, the outermost one lying next to the epidermis. ×192.

Fig. 3. Section of a young nucellus showing four conspicuous cells. ×192.

Fig. 4a. An enlarged conspicuous cell, evidently, the mother cell. ×192.

Fig. 4b. Section of the entire ovule of figure 4a. ×44.

Fig. 5. Section of the nucellus of an older ovule, showing only one conspicuous cell, deeply embedded in nucellar tissue. ×192.

Fig. 6. Median section of the nucellus of an older ovule, showing the nucleus of the mother cell in synapsis. ×434.

Fig. 7a. Megaspore mother cell with nucleus in synapsis having consumed most of the nucellar tissue. ×434.

Fig. 7b. Section of the ovule shown in figure 7a. ×44.

Fig. 8. Median section of nucellus with mother cell deeply embedded. ×192.

Fig. 9. First division of the mother cell. ×434.

Fig. 10. Longitudinal section of nucellus, showing linear series of megaspores, the innermost one functioning. ×434.

Fig. 11a. Median section of nucellus showing first division of functioning megaspore, and an evidence of a cell wall forming between the nuclei. ×434.

Fig. 11b. Section of ovule shown in figure 11a. ×44.

Fig. 12. A two-nucleate embryo sac, all evidence of cell wall having disappeared. ×192.

Fig. 13a. The four-nucleate embryo sac growing into the micropyle. ×192.

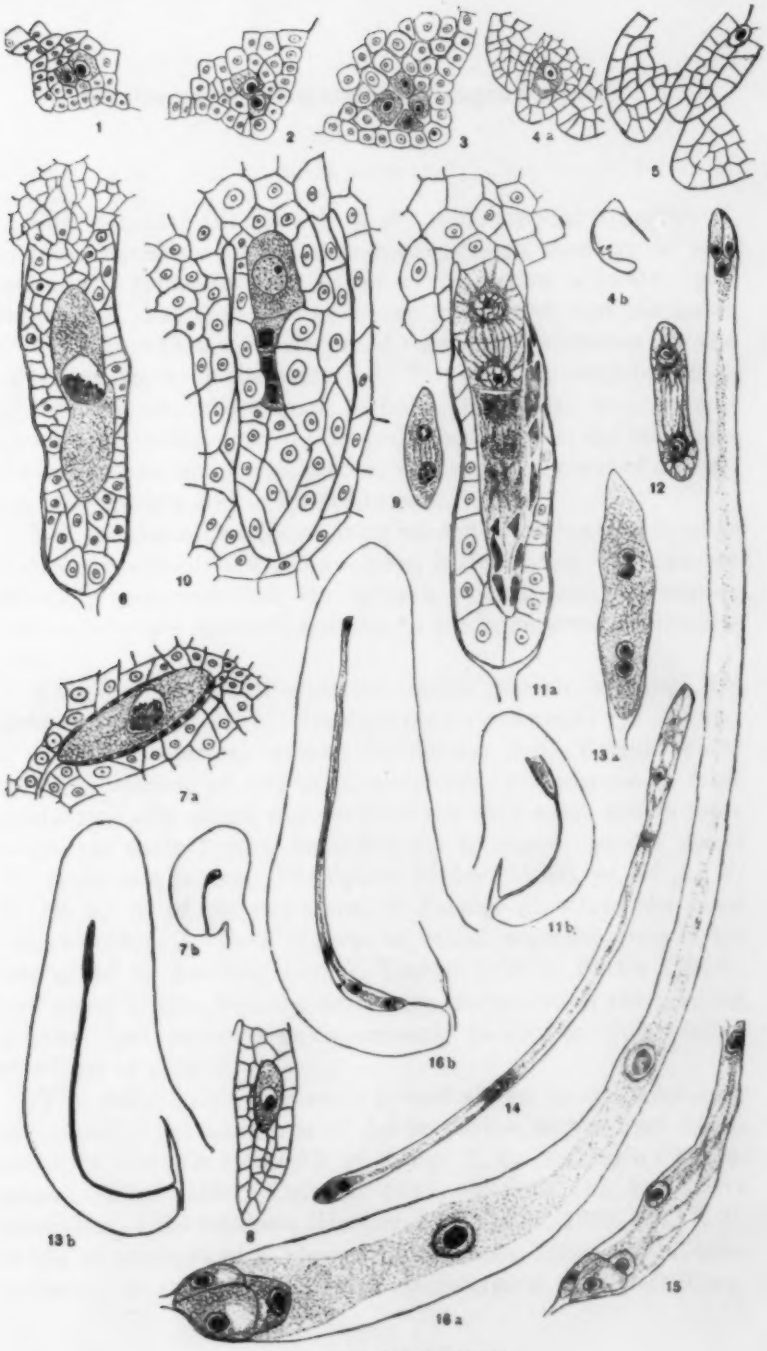
Fig. 13b. Section of the ovule of figure 13a showing long, curved micropyle. ×44.

Fig. 14. An eight-nucleate embryo sac before the organization of the egg apparatus. ×192.

Fig. 15. The micropylar end of an embryo sac, after the organization of the egg apparatus. ×192.

Fig. 16a. A mature embryo sac before fertilization. ×192.

Fig. 16b. Section of the ovule of figure 16a showing egg apparatus very near the outer end of the micropyle. ×44.



IPOMOEA TRIFIDA

Studies on morphogenesis in fungous mycelia

ILLO HEIN

(WITH PLATE 15)

The fact that the growth of the main hyphal branches of fungous mycelium in a fairly homogeneous medium is predominantly radial has not, so far as the author is aware, been emphasized, but that it *is* generally radial and that the habit of radial growth is of widespread occurrence is shown by the numerous figures in the literature. Not only the main branches of a fungus mycelium grow radially, but there is a general tendency to radial orientation and symmetry in the structure of carpophores, ascocarps, etc., as well as in the parts of numerous other plants and in lower animals.

The spontaneous self-orienting tendencies of fungous hyphae in their growth directions have been little studied. It is rather generally assumed that the growth orientations of fungous hyphae are very specially subject to environmental determination.

Excellent figures illustrating radial growth in fungi are given by Brefeld (1877) for *Coprinus stercorarius* (*pl. 1, figs. 2, 4, 5*) and *Agaricus melleus* (*pl. 10, figs. 1–5*). Brefeld traces the development of *Coprinus stercorarius* from spore to fruit production and shows that both in the very early and in later stages the main hyphal branches are arranged radially about the spore as a center. The figures of Zopf (1880, *pl. 14, fig. 4; pl. 19, fig. 5*) of the mycelium of *Fumago* illustrate the same radial tendency. Good figures of radial mycelial growth are also given by Leonian (1926), Tisdale (1917), Porter (1924), and many others, but one finds little discussion of the relating internal and external environmental factors in determining this form of growth.

The radial habit of growth is well shown in the secondary mycelium of the ascocarps of the Sordarias, as has been illustrated by Woronin (1869–70, *pl. 2, figs. 7, 9*), in certain Chaetomiums (Zopf, 1860; Chivers, 1915), and in the vegetative mycelium of the mildews (Harper, 1895; Hein, 1927, *figs. 1, 2*), in the appendages of mildews (the Tulasnes, 1853; and all later authors), in the germ tubes of *Megalospora affinis* (DeBary,

1884, *fig. 57 f.*), in the initial enveloping hyphae of *Pyronema*, (Tulasne, 1851; DeBary, 1863; Harper, 1900), *Sphaerotheca* and *Erysiphe* (Harper, 1895), in the mycelium of the pileus in fleshy fungi (Atkinson, 1906; Blizzard, 1917; Levine, 1913, 1914), and in the gills of agarics (textbooks of botany). In the higher plants, and in such animals as the old group Radiata, the well established facts of radial 'perimeric' symmetry, exotrophy, etc. have been the subject of more intensive study. Still the voluminous literature on the tropisms in plants yields little data concerning radial growth.

Sachs (1882) pointed out that the medullary rays in stems are perfectly radial in their orientation and notes that this growth habit is dependent upon the manner in which the cells of the cambium ring divide.

It was Noll (1894) who first made the radial growth of lateral plagiotropic roots the subject of intensive experimentation and on the basis of experimental data proposed an hypothesis which, so far as I find, has not been challenged. Noll grew lupine seedlings in liquid culture solutions under conditions in which the roots were supposed to be in a practically homogeneous environment. No mechanical or other barriers were present and the solution was presumably uniform in concentration throughout. Noll found that in such cultures the lateral roots grew radially outward from the main axis. Directly in the path and at right angles to the growing lateral roots pieces of glass were then placed so that the roots were compelled to alter their direction of growth. Under these conditions the roots followed the surface of the glass, maintaining their plagiotropic plane until they reached its edge, where they abruptly followed a new direction of growth which was found to be in a direction radial to their point of origin, i.e. radial to the main tap root as a centre.

Noll (1900) concludes that besides being sensitive to numerous external environmental stimuli, plant organs are also sensitive 'für Form und Lage des eigenen Körpers,' which acts as a stimulus. The plant form as a whole exerts a stimulus which may influence the form of any of its parts. This capacity Noll called *Morphästhesie*. According to Noll the directions of growth in such a case are apparently due to inner form determining factors. It appears that Noll (1896) believed all

forms of radial growth are due to internal form determining factors, as is shown in the following passage:

> Wie eine Aktinie unter normalen Umständen das Bestreben zeigt alle ihre zahlreichen Arme in radialer Richtung von sich wegzustrecken, so scheine auch dem Pflanzenkörper (den ich physiologisch im Ganzen als einen individuellen Plasmakörper auffasse, (wie Sachs auch in morphologischer Hinsicht thut) eine Art inneren Empfindungsvermögens (Ich denke dabei nur an Reizempfindlichkeit, nicht etwa an ein dunkles Bewusstsein) von gegenseitigen Stellung seiner Organe innezuwohnen.

The literature on the relations of plant form and response to environmental stimuli is voluminous and has been many times reviewed. Relatively little work has been done in this connection on the fungi. The response of the carpophores of fleshy fungi to light and gravity have been many times studied, and reviews of the literature are given by Levine (1914), Blizzard (1917), and Atkinson (1906). The histogenetic and morphogenetic processes concerned in development of the carpophoral form have been studied by Brefeld (1877), DeBary (1884), Atkinson (1906), W. Magnus (1906), Blizzard (1917), Levine (1913, 1914), Walker (1919) and Hein (1928). Responsiveness in fungous hyphae has been studied by Küster (1908), Stevens and Hall (1909), and Liesegang (1920). Most of the studies of hyphal reactions and interactions have been made from the standpoint of hyphal anatagonisms. Porter (1924) recently reviewed the data in the literature, and on the basis of his own observations made five groups of hyphal inhibitions which he designated as types A, B, C, D, and E: A, mutually intermingling, B, overgrowing, C, slight inhibition, D, growth around, E, inhibition at a distance. Porter's figure 1, plate 6, illustrates the reactions of radially growing hyphae to a rectangular, sterile block of agar placed before them, but on the mechanical inhibition involved there is no comment in the text. There appear to be formed at the edges of the agar block new centres from which the hyphae grow radially. The barrier in Porter's figure was placed at right angles to the radial hyphae which were either inhibited or compelled to grow in a new direction. They appear to have grown around the barrier, and then after having passed around it, tended to grow more or less inward in all directions from the opposite ends and on the peripheral side of the barrier. The photograph does not show clearly the directions of growth of the individual filaments.

OBSERVATIONS

In the attempt to analyze further the form determining factors in a mycelium and especially to distinguish the effects of external environmental from the so-called rektipetiotic factors, I have made experiments on the behavior of hyphae when they come in contact with mechanical barriers. I have worked for the most part with *Sordaria fimiseda* and a species of *Chaetomium*. My observations were made largely on cultures in petri dishes and in Van Tieghem cells.

The ascospores of *Sordaria* and *Chaetomium* germinate readily under ordinary room conditions and never seem to need any special stimuli to induce growth. Clean, ripe ascospores of *Sordaria* were obtained from ripe ascocarps in the following manner: shortly before spores were desired the petri dish covers were cleaned and sterilized with alcohol and replaced on the cultures. In from ten to twenty minutes one can find abundant ascospores which have shot from the ripe asci against the covers, where they are held fast by their gelatinous envelopes. Clean, fairly sterile spores were thus obtained. Single spores were then removed from the covers with a flamed needle, the spores adhering readily to the needle with a little manipulation. I have found this method of obtaining single spores far more efficient and speedy and the percentage of contaminations smaller than with other well known methods, such as the use of the Barber pipette, or the method used by Edgerton (1915).

I do not find that the ascospores of the species of *Sordaria* and *Chaetomium* which I used require moist earth or dung decoction or any other specific medium for their germination, as reported by Woronin (1869-70, p. 341). They germinate easily under a variety of conditions, even in a moist atmosphere. In fact they germinate so rapidly after ejaculation from the ascus that, unless the spores are collected from the cover dish within about half an hour, so many of them will have germinated that the isolation of spores for culture is very difficult. Possibly their gelatinous envelopes contain sufficient moisture for their germination.

I find the appearance of the ascospore of *Sordaria* on germinating is identical with that described by Woronin (1869–70, p. 341): from the 'Keimporus' at one of the ends of the spore a spherical germ tube is produced and this then gives rise to from

one to five mycelial hyphae which grow very rapidly in radial directions.

The main hyphal branches continue to grow radially, branch profusely and become septate. The secondary, tertiary, and later branches all tend to grow radially away from the spore as a center. The angles formed by these branches with the main hyphae are not always the same, they vary between an acute and a right angle. The dense mass of mycelium is from the beginning more or less circular in outline. In the very early stages there is a tendency for the margin of the colony to be very slightly wavy, due to irregularity in the rate of hyphal growth, but this soon disappears and the margin becomes even, giving a perfectly circular outline to the colony. The smooth, clean cut, circular outline of the whole colony is striking.

At about seventy-two hours the mycelial growth in the cultures of *Sordaria* attains a diameter of about 7 mm. These hyphae are entirely imbedded in the substrate and not very conspicuous to the unaided eye. At this time, the dense aerial mycelium appears suddenly and grows rapidly, producing a hemispherical tuft. The aerial mycelium soon attains a height of about 5 mm. in the center. When the colony attains a diameter of about a centimeter the hyphae in the center seem to collapse. The aerial mycelium immediately after its appearance spreads radially with and at the same rate as the substrate mycelium, and as the aerial hyphae in the center collapse a wide ring is produced. As the ring is widened by the radially growing marginal hyphae distinct concentric zonation appears. The rings which consist of alternating less dense and more dense hyphal growths have a width of from three to four millimeters. The concentric zones in this stage are of the type described by Stevens and Hall (1909). The dark zones are due to crowding of the filaments through repeated branchings, while the lighter zones are due to the smaller number of hyphae. The surface of a cross section through such a colony would have a wavy outline.

When the mycelium has attained a diameter of about 3 cm., usually after from five to eight days, very small white irregularly placed dots, the young ascocarps, appear in the central area. The young ascocarps appear under the lens as an aggre-

gate of interlaced hyphae with numerous radially arranged hyphae around them. These hyphae grow radially from the ascocarp and are in the early stages equally radial in all planes, in the substrate as well as in the air (figure 18). A study of the further growth and development of the ascocarp of *Sordaria* is to be described later.

No zonation appears in the distribution of the first formed ascocarps in the central region of the colony, but outside this region the alternation of concentric rings with numerous ascocarps and less fertile areas in which there are fewer ascocarps is conspicuous. These rings have about the same width as the previously described rings of dense and less dense hyphal growth. The distribution of ascocarps is by no means limited to the specially fertile zones: they grow all over the substrate, but tend, as has been universally noted, to be more numerous in alternating zones. Such phenomena have long been known in the growth of fleshy fungi, where the concentric zones of carpophores are popularly known as fairy rings, devil's gardens, etc. The most recent review of the literature on this point has been given by Shantz and Piemeisel (1917). Shortly after the production of ascocarps, secondary mycelial hyphae grow radially and profusely from the ascocarp, become prominent and form a white fringe surrounding the black pyrenocarp.

Stevens and Hall (1909) have figured and described the localization of the sclerotia of *Sclerotinia Libertiana* in concentric rings. The sclerotia are more abundant in a zone midway between two adjoining mycelia. Zonation in the formation of conidiophores is well shown in the alternating green and white concentric rings in cultures of *Penicillium*.

The ascocarps of *Sordaria fimiseda* which I have studied are formed most abundantly in the region where two mycelia meet. The more abundant production of ascocarps between two mycelia in this case is not the expression of heterothallism, as might appear from the cultures. *Sordaria fimiseda* is homothallic, fruit production resulting from the mycelium produced by a single spore.

Though no elaborate experiments were made to test the effect of gravity on radial growth of *Sordaria* mycelium, the few simple tests carried out indicate that gravity has little or no effect on the circular outline of the colonies. Petri dish cultures

of *Sordaria* were placed on edge and kept in this position until the mycelium completely covered the substrate.

Measurements of the length of the horizontal and vertical radii of the cultures placed on end were made from time to time as the colonies enlarged, and in no case did the measurements reveal differences in rate of growth. While the general outline of the colonies remained apparently unaffected by gravity, the aerial mycelium on the other hand seemed to give slight evidence of a positive response to it. In the lower half of the colony the aerial hyphae are all very similar and grow in a generally radial direction, like those in the colonies kept in the horizontal position, but in the upper half the aerial mycelium, while it presents a generally radial direction of growth, shows hyphae that are irregularly bent in various directions.

Whether radial growth of hyphae is due to external environmental factors, to morphaesthesia, or to rektipetiotic factors has never been shown. Noll's (1894) experiments and results with roots suggest the possibility of similar studies with fungi.

Single spore, two spore, and multispore cultures of species of *Sordaria*, *Mycogone*, *Chaetomium*, and of *Monilia fimicola* were made in hanging drops for observing the early stages of growth.

Typically the hyphae of *Chaetomium* show the following growth orientations: two hyphae are produced from nearly opposite sides of the spherical bulb-like germ tube described by Zopf (1881) and grow rapidly in a direction at about either 150° or 90° to the long axis of the spore (fig. 1). When the angles made by the hyphae are about 150°, a third hypha grows from the germ tube in the direction of the long axis of the spore (fig. 2). This third hypha apparently grows more rapidly and soon attains a length equal to that of the pair first produced. All three then grow at about an equal rate. They are thus about equally spaced about the spore and radial from the very beginning. When two hyphae are produced at right angles to the spore axis, as is often the case (figs. 1b, 3), a branch appears on each hypha and on the same side as the spore about 70–80 microns from it. Such branches grow rapidly at right angles to the hyphae from which they arise (fig. 4, *a* and *b*). Seventy microns further on each main hypha a branch grows in the

opposite direction to the previous two branches (figure 8, *a* and *b*). These two methods of branching I find most common in the early stages although there are numerous variations of these, as well as other more distinct methods. Whatever the initial arrangement of the main branches may be, the tendency is for the hyphae always to be disposed radially about the spore (figs. 5, 6, 7, 11, 12, 14). With two (fig. 9) or more spores (fig. 10) the direction of growth becomes more conspicuous. Possibly the main hyphae are mutually repellant even at a distance from one another. Some evidence on this point is given in figures 4, 15, 17, and 11. In figure 11 it appears that lateral branching from two parallel main hyphae is more or less suppressed on the sides facing one another. On the sides *a* and *a'* of the hyphae *b* and *c*, figure 11, the branches appear in abundance, while on the sides of the hyphae facing one another there are almost no branches. After the point where the two branches *b* and *c* cross one another at *x*, branching seems not to be confined to any particular side, and apparently there is here no hyphal antagonism at the distance involved. The two branches *b* and *c* are not actually touching each other at *x*, but are very close together. I have never observed primary branches of this fungus crossing or actually touching one another. Secondary, tertiary, and later branches in older cultures are frequently very close and cross each other repeatedly. In figure 11 *b* and *c* are secondary hyphal branches. Figure 17 shows some twenty spores arranged in a straight line. The development of hyphae is most profuse and in a direction at right angles to the line of spores. None of these main branches are in contact. They all grow more or less parallel to each other. It would appear that they are mutually repellant, and that the antagonism keeps them in their parallel course. The radial arrangement of the secondary mycelium of *Sordaria* shown in figure 18 may also be due to mutual antagonism. The young ascocarp shown is completely imbedded in the substrate and the secondary mycelium grows radially in every direction from it.

Where several colonies of *Sordaria* are growing in a single dish, the hyphae are inhibited in their growth where the colonies meet. The inhibition is most marked where the hyphae from opposite colonies approach each other in a straight or nearly straight angle and becomes less marked as the angles of

approach grow smaller. The inhibition in *Sordaria* in this case appears to be of the E type described by Porter (1924).

In order to contribute to our understanding of radial growth and to determine whether it is due to external stimuli, or to internal rektipetiotic conditions (Lindau, 1899, Pfeiffer, 1925), mechanical barriers were placed at right angles to and directly in the path of the advancing main branches so as to force them to change their direction of growth. Several kinds of barriers were tried. Very small, thin, flat, rectangular pieces of mica (1×2 mm.) were inserted into the agar at right angles to and at varying distances in front of the growing point of an advancing hypha. The successful preparation were not very satisfactory except for mass cultures, and the method was finally discarded for the present studies. A second method consisted in stirring small particles of sand and spores in the culture medium so that some of the particles would by chance be placed in the desired positions. The sand was first crushed in a mortar in order to obtain small angular grains showing flat surfaces corresponding to the cleavage planes. The finest particles were then separated from the larger by stirring both in water, the water containing the particles which remained suspended a few seconds was then poured off and evaporated, leaving the fine angular grains in the dish. The fine angular particles thus obtained, together with the spores, were stirred into the culture medium and placed in a Van Tieghem cell. In this way a purely random placement of barriers was obtained, but a sufficiently large number of these were found in the positions desired.

When a hypha approaches a barrier it is apparently unaffected in its direction of growth until it comes in actual contact with it. The hypha then follows the contour of the obstruction on the side which forms the widest angle with the axis of the hypha. I have not yet studied the reaction to barriers which were placed at exactly 90 degrees to the axis of the hypha. The hypha continues its growth around the barrier, remaining in close contact with it until a point is reached where there is no longer an obstruction to its original direction of growth. It then turns from the barrier, growing in a new direction which is parallel to the radius from the spore as a center. Figure 16 illustrates the typical growth of a hypha around and past such an interposed barrier. In this case a single main branch de-

veloped from the germ tube and grew in the typical direction at right angles to the long axis of the spore until it reached the barrier, where its course was diverted to the left. The left side in this case formed the widest angle with the original axis of growth of the hypha, and then the course *m-o* was followed until the direction of growth, parallel to the original, *g-m*, was no longer obstructed. The hypha then continued to grow to point *x* in a direction not quite parallel to its original course but parallel to a radius from the center of the spore. At *x* the hypha turned slightly to the left, owing probably to some environmental cause.

In figure 12 the hypha *a* (enlarged view in fig. 13) has grown under a barrier. The original direction of growth was resumed after the barrier was passed.

In the case shown in figure 14 (enlarged view in fig. 15) the course of the hypha seems to have been diverted to the right of the barrier even before actual contact was made. There are here two barriers, a smaller one *x* preceding the larger *y*. It would appear that the barrier *x* caused the hypha to be diverted to the right even before actual contact was made. The barrier *y* presented a contour which allowed the hypha to grow in its original plane parallel to the substrate. At *r* the hypha grew over and around the barrier and then tended to grow to the left, apparently to resume its radial direction, and then grew under the barrier at *r'*. After the sand particle was completely passed the hypha resumed a direction of growth approximately parallel to its original path.

Macroscopic studies were made of hyphae meeting in their growth barriers made of rectangular pieces of mica inserted in the agar so that they were tangent to the circular colony when the hyphae reached them. The observations were made only on the profusely growing aerial mycelium. As noted, its behavior is, so far as radial habit is concerned, quite similar to that in the mycelium of the substrate. On reaching such a barrier some of the hyphae grow upward and over it, and on reaching the opposite side they continue their radial growth. Immediately after reaching the top of the barrier the hyphae grow horizontally a short distance (.5–1 mm.), but their course is soon diverted downwards toward the substrate, where they continue in the radial direction. There is a limit to the height to

which the hyphae will hurdle such barriers. Barriers higher than 3mm. proved to be too high and the hyphae merely mass themselves before the barrier. Many hyphae which do not grow over the barriers, especially those near their ends, tend to grow around them. They turn either to the left or right.

That these hyphae are not plagiotropic, as would appear from figures 13 and 15, becomes apparent from petri dish cultures kept in vertical positions. The substrate mycelium is in every respect similar to that grown in cultures kept in horizontal position. The mycelium in the substrate of a vertically placed culture radiates usually in all directions; downwards, horizontally, upwards, and in every direction between these extremes. All mycelial hyphae of *Chaetomium* appear to be unaffected by gravity, but will, when other conditions are equal, grow with similar profusion in *all* directions. Further evidence on this point is reserved for a future study.

DISCUSSION

It is commonly held that the directions of growth of plant organs are due largely to external stimuli, such as light, gravity, temperature, and chemical stimuli. In a growing tap root the gravity stimulus determines the downward growth. Secondary roots grow at right angles or obliquely to gravity, while tertiary roots grow in all directions. In a dry soil roots tend to grow toward moist parts. The radial directions of growth in the lateral roots of lupines, as observed by Noll (1894), cannot be attributed to the above stimuli, since the medium in which they grew was fairly uniform throughout. The stimuli which produce the radial growth are perhaps to be sought in the plant itself. According to Schwendener (1878), during the plastic growing stage of an organism the production of a large number of organs or parts of organs on a limited area of the plant body results in a crowding, shoving, and sliding of cells and cell groups over one another. Movements then take place through growth or reduction of lateral organs which result in the most exact orientation of parts. The position of an organ on the plant body is, according to this conception, due to mechanical necessity.

Where a number of spores germinate in a limited area, it is obvious that the crowding of the young hyphae may produce

a radial orientation about the spores. If we assume that fungous hyphae are mutually negatively chemotropic (Müller, 1922), and there is some evidence that many are so (figs. 17, 18, and Delitsch, 1926, fig. 2), continued radial growth would be the natural result. Crowding, competition for food, and mutual antagonism would fail, it seems to me, to account for the radial orientation of hyphae about a single spore. Possibly in the very early stages when the distance between the hyphae is relatively small, hyphal antagonism at the distances involved may play a part in their orientation, but the rapid radial growth away from the spore soon increases the distance between the ends of the radii to the point where mutual negative chemotropism seems improbable. Radial growth of lateral roots in the early stages may possibly be due to a mechanical adjustment, while the continued radial growth may be due to rektipetiotic factors. However, I am unable to connect this view with the behavior of fungous hyphae. Fungous hyphae, if not perfectly radial in the very early stages, as for example in figures 3 and 4, become radial as soon as other hyphae are produced. There does not appear to be any mechanical necessity in the radial orientation of the hyphae about the spore in cases of this kind.

Czapek (1900, p. 307) stated that, generally speaking, a plant has no organs of sensation and the whole plant or an organ or a tissue may respond to external stimuli. This 'Empfindungsvermögen' Czapek termed aesthesia, which, according to the external stimulus, is known as geoaesthesia, photoaesthesia, chemoaesthesia, mechanoaesthesia, hydroaesthesia, etc. Noll (1894, 1900) showed that the radial growth in the secondary roots of lupines is not due to stimuli which could be classed under any of the known stimuli, suggested that the form and position of the organism as a whole acts as a stimulus to its parts, and proposed the term morphaesthesia for the process which produces the radial growth in lateral roots.

The possibility that Noll's morphaesthesia is an expression of surface tensions is to be considered. Noll (1903, p. 403) himself appears to be inclined to this view and states:

> Es variieren die Oberflächenkräfte——nicht nur mit der jeweiligen Gestalt, sondern bei gleicher Form auch mit der absoluten Grösse derselben, so dass alle Form- und Grössenverhältnisse eines Organismus in bestimmten Oberflächenspannungen zum Ausdruck kommen müssen, die man als 'mor-

phostatische Oberflächenspannung' oder kurz als 'Formspannung' bezeichnen kann.

Küster (1913), however, is of the opinion that tissue building processes are not to be explained in the light of surface tensions any more than are the varying figures which are exhibited in the borders of Liesegang 'Diffusionsfelder' in gelatine cultures.

The radial arrangement of organs on the plant or animal organisms in early stages may be due to their orientation about the plastic cylindrical or spherical body. The cylindrical or spherical shapes owe their form to the fact that they are sufficiently plastic, or were so in the early stage, to permit the free expression of least surface configurations.

The very striking fact about Noll's roots, however, is that the radial growth is persistent at a considerable distance from the main tap root and that the radial direction is resumed after the original radial direction has been altered. That this resumption of the radial direction is due to the interaction of surface forces is difficult to see.

In my cultures of fungous hyphae I have shown that the hyphae behave in a manner very similar to Noll's lateral roots, and I am inclined to believe with Noll that the radial direction of growth is due to some such form tensions or stimuli as morphaesthesia.

The author is greatly indebted to Professor R. A. Harper for the criticisms and suggestions he has so kindly given.

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Explanation of plate 15

All figures were drawn with the Abbe camera lucida. Figures 8, 10–12, 14, 16, and 19 are magnified approximately 56 diameters; all other figures are magnified approximately 450 diameters. Unless otherwise mentioned the figures are of species of *Chaetomium*.

Fig. 1. Early stages in the germination of *Chaetomium* spores, spherical germ tubes with one or two hyphal branches.

Fig. 2. Later stage showing three radially arranged main branches.

Fig. 3. Early stage with only two main branches.

Figs. 4 and 5. The secondary branches have begun to appear.

Figs. 6 and 7. Later stages with well developed secondary branches. General direction of growth of the primary secondary branches is radial.

Fig. 8. Only two main primary branches have grown radially.

Fig. 9. More pronounced radial growth of the mycelium produced by two or more spores.

Fig. 10. Thirty or more spores grouped together. The colony shows conspicuous radial growth of the main mycelial branches.

Fig. 11. Shows absence of mycelial development from the adjoining sides of secondary branches *b* and *c*. On the opposite sides a^1 and *a* there is abundant growth.

Fig. 12. A main branch, *a*, has grown under a barrier and has resumed its original radial direction of growth.

Fig. 13. Enlarged view of hypha *a*, of figure 12.

Fig. 14. Behavior of hypha toward a barrier.

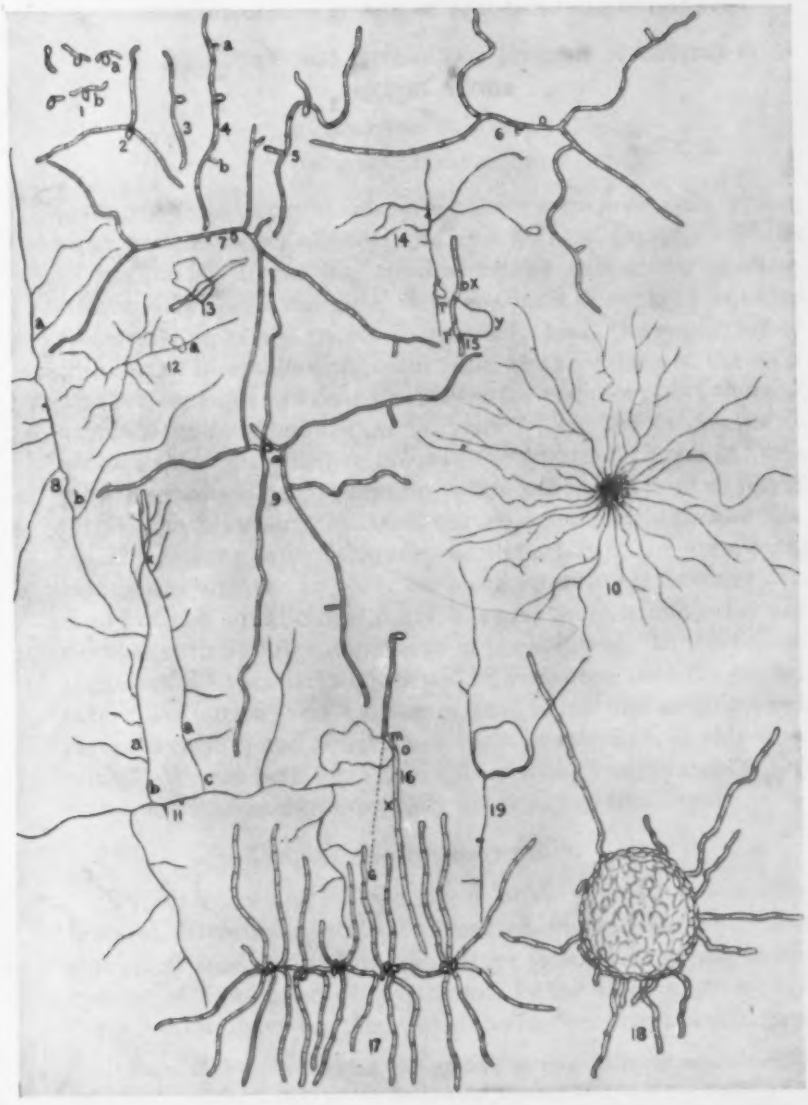
Fig. 15. Enlarged view of hypha from figure 14. The hypha has first encountered a small barrier at *x* and then grown over a projection of the larger barrier *y* at *r* and under a second projection at r^1. Radial growth was resumed after point r^1 was passed.

Fig. 16. A main hypha diverted from its original course (*m-g*) by the barrier, has grown around the barrier at *m* to *o*, and then followed a new direction which was radial to the spore as a centre.

Fig. 17. Some twenty spores arranged in a straight line. All hyphae tend to grow at right angles to the line of spores, and without touching, grow parallel to each other.

Fig. 18. Young ascocarp of *Sordaria* in three-dimensional nutrient medium, showing secondary mycelium growing radially in all directions in the substrate.

Fig. 19. A main branch and a secondary branch, after passing a barrier, have resumed directions of growth which are radial to the spore as a center.



HEIN: MORPHOGENESIS IN MYCELIA

UNIV. OF

Studies on the growth of root hairs in solutions

VIII. Structural and intracellular features of collards in calcium nitrate

CLIFFORD H. FARR

(WITH THREE TEXT FIGURES)

In the sixth paper of this series[1] there were presented certain structural responses of roots and root hairs of Georgia collards to various hydrogen-ion concentrations and molar concentrations of calcium chloride. The responses of the root included the wrinkling of the cortex in acid solutions, the rupturing of the cortex in alkaline solutions, and the zonations of the root. The responses of the root hairs were for the most part those of amphibious root hairs, that is, hairs which had originated in air and then continued to grow in the solution. Some of these grew normally after immersion, while others took on different forms such as swollen, inflated, curved, capitate, branched, etc.

The present paper includes a similar study of the same plant in calcium nitrate. In this case more attention is devoted to a study of the aquatic root hairs, that is, those which arise and develop entirely after immersion in the solution. In the following paper (IX) statistical data will be presented as to the growth rate, distribution, and spacing of root hairs, and as to growth rate, curvature, and zonation of roots in solutions of this compound. We are here concerned rather with types of data which do not lend themselves so readily to statistical treatment.

SPACING OF ROOT HAIRS

Typical views of the spacing of aquatic root hairs in solutions of calcium nitrate are presented in figure 2, *1–4*. The statistical study will show that there is wide variation in the spacing of hairs upon different roots in the same solution; but there is a tendency for the hairs to be farther apart in acid than

[1] Farr, C. H. Studies on the growth of root hairs in solutions—VI. Structural responses to toxic pH and molar concentrations of calcium chlorid. Am. Jour. Bot. **15**: 171-178. 1928. The complete series is listed in connection with no. VII, Bull. Torrey Club **55**: 223. May 1928. The present paper has been prepared for publication by Mrs. Wanda K. Farr since the sudden death of the author on 11 Feb. 1928.

in alkaline media, with neutral solutions having an intermediate relationship. The drawings here shown are, therefore, not to be considered as being merely typical of the concentrations in which the particular root sketched was growing. They repre-

TABLE 25

Forms of amphibious hairs of collards in calcium nitrate

(*a*) *Hydrogen-ion concentrations*

pH	n	und	inf	swo	cur	sic	ng	bra	kin	cap	coa	bur	spa	fla	cro	slo	bea	Total
4.0			+									+						2
4.5	+	+	+		+		+		+	+	+		+		+			10
5.0	+	+	+	+	+	+									+			7
6.0	+	+	+	+	+	+		+	+	+		+	+	+				12
7.0	+	+	+	+	+	+	+	+	+	+	+			+				12
7.5	+	+	+	+	+													5
8.0	+	+		+	+	+	+	+	+	+	+							10
9.0	+	+	+	+		+	+	+		+								8
9.5	+	+		+		+												4
10.0	+	+	+	+	+	+	+	+	+		+					+		11
10.5	+	+		+	+	+	+	+	+		+	+				+		11
11.0	+			+			+	+									+	5
11.5	+	+	+									+						4
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
FpH	12	11	9	10	8	8	7	7	6	5	5	4	2	2	2	2	1	

(*b*) *Molecular concentrations*

M	n	und	inf	swo	cur	sic	ng	bra	kin	cap	coa	bur	spa	fla	cro	slo	bea	Total
0.004	+	+	+	+	+	+		+			+			+			+	10
0.008	+	+	+	+	+	+	+	+	+	+	+		+		+			13
0.012	+	+	+	+	+		+	+	+		+	+	+	+		+	+	14
0.020	+	+	+	+	+	+	+	+		+		+						10
0.030	+	+	+	+		+				+		+				+	+	9
0.060	+		+	+	+	+	+			+								7
0.100	+		+				+											3
0.149	+						+											2
	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
FM	8	5	7	6	5	5	6	4	2	4	3	3	2	2	1	2	3	

+ indicates the occurrence of the form of hair indicated by the symbol at the top of the column in the solution indicated at the left.

FpH refers to the frequency of each type in the various pH concentrations; n, normal appearance; ng, no growth; inf, inflated; swo, swollen; und, undulated; cur, curved; sic, sickle-shaped; bra, branched; kin, kinked; spa, spatulate; cap, capitate; fla, flasked-shaped; cro, crooked; slo, sloped; bur, burst; coa, coagulated; bea, beaded.

sent, rather, different types of distribution of hairs, more than one of which might be found in a single solution. Eleven hairs are shown in each sketch, beginning with the smallest hair at the right-hand side. The drawings are all made to the same scale. They show that the hairs are by no means equidistant,

though this condition is more closely approached where the spacing is greatest (fig. 2, *1*). On the other hand, they are frequently clustered in pairs, threes, or even fours or fives. In these cases, whether more than one hair arises from a single superficial root cell cannot be ascertained without sectioning. That more than one hair may arise from a single cell is clearly shown in some instances (fig. 2, *3*), which will be described below. The solutions in which the hairs sketched were growing are as follows: (1), 0.060 M. at pH7; (2), 0.060 M. at pH 4.5; (3), 0.060 M. at pH 9.0; (4), 0.004 M. at pH 7.5. While there is a wide range of variation as to the spacing of the aquatic root hairs in any given solution, it may be stated in general, that in neutral and aicd solutions of high salt concentration there is a tendency to equidistant spacing; in alkaline solutions and in solutions of low concentration there is tendency toward clustering of these root hairs.

FORMS OF AMPHIBIOUS ROOT HAIRS

The amphibious root hairs present a great variety of forms, the number being even greater in nitrate than in chloride, as shown in table 25. In all solutions studied there were amphibious root hairs which appeared *normal* in shape, except in pH 4.0. It does not follow, however, that in all these solutions, root hairs previously growing in the air continued to grow in the solution without change of form. In fact it was observed that some of these supposed amphibious root hairs did not grow at all after immersion in many of the solutions. No such hairs were noted in 0.004 or 0.030 M. calcium nitrate, nor in any concentration of this salt at pH 5.0 or 6.0. This does not mean, that such were not present in these solutions, inasmuch as no great effort was made to ascertain whether apparently amphibious root hairs were growing after immersion. It is, of course, a misnomer to refer to root hairs which did not continue to grow after immersion as amphibious: they should rather be called *aerial* root hairs.

In 0.140 M solutions root hairs which had appeared before immersion failed to grow thereafter. Hence all root hairs in this, the highest molar concentration studied, were either aerial or aquatic. We thus have a case of toxicity becoming so extreme that it obliterates the amphibious habit, while still

permitting the origin of new hairs and their growth at a slower rate. The amphibious hair which changes form after immersion is an example of a structural expression of shock. If, as occurs in the swollen type of amphibious hair (fig. 1, *2*), the hair later resumes its original diameter and direction, we have an illustration of complete recovery from shock. If the hair continues to grow, however, at a new diameter, as in the inflated type (fig. 1, *1*), or in a new direction, as in the curved type (fig. 1,*9*),

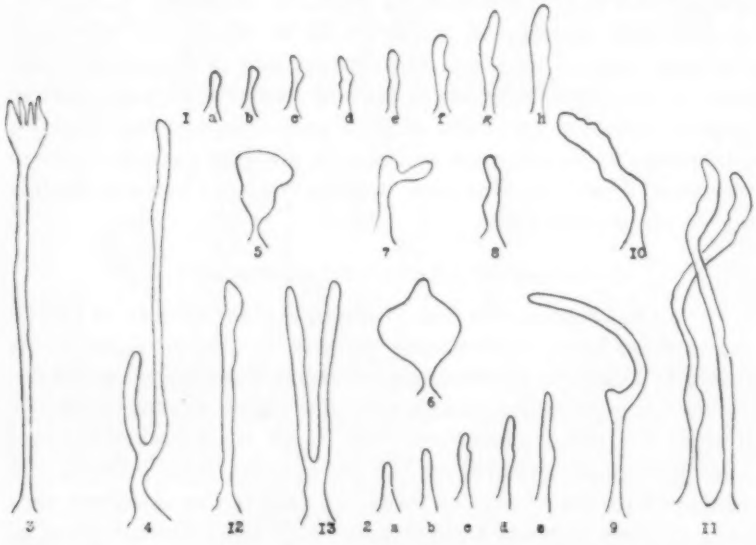


Fig. 1. Abnormal root hairs of collards in solutions of calcium nitrate (description in text).

we have a modification which may be interpreted as an adaptation to a new environment.

In 0.100 M calcium nitrate there were three types of root hairs; aerial, inflated amphibious, and acquatic. Thus we have an expression of a lower degree of toxicity than that produced by the 0.140 M solution. It would seem from this that the inflated type of root hair is the one which indicates the highest degree of toxicity; that is, if a solution will not support the growth of inflated root hairs it will not support the growth of any amphibious hairs; and some solutions are so toxic as to permit the formation of inflated hairs as the only type of am-

phibious hairs. This is further indicated by the results in calcium chloride (fig. 3), and by the fact that inflated hairs were also found in the most acid solution studied, pH 4.0, and in the most alkaline solution, pH 11.5. They were, however, not found in pH 8.0 or 10.5 or 11.0, which indicates that they are rather rare in very alkaline solutions. Nevertheless they were perhaps the most common type of modified amphibious hair observed.

Swollen hairs, (fig. 1, *2*), that is, those which enlarge at the tip upon immersion and then resume their original diameter, were found in all concentrations studied, except 0.100 and 0.140, and in all pH values, except 4.0, 4.5, 9.5, and 11.5. It may be concluded, therefore, that they are characteristic of a lower degree of toxicity than are the inflated ones, since they do not occur at the two highest concentrations, nor at either the extreme acid nor at the extreme alkaline limits of growth.

From the standpoint of frequency of occurrence, the third type of abnormality observed in amphibious root hairs was that designated as *undulating*. This type consisted of a wavy form, which differed from the beaded type, listed below, in that the bulge on one side is opposite a depression on the other, instead of having the bulge opposite, and alternating with depressions which are also opposite. They were seen in all concentrations of calcium nitrate up to 0.060, but were not found in this or higher concentrations. They occurred in all pH values except 4.0 and 11.0. They thus seem to be produced by low or medium concentrations which are not too acid or alkaline. They thus represent a still milder degree of toxicity than the swollen, especially as to molar concentration.

Curved root hairs were found in 0.004, 0.008, 0.012, and 0.060 M concentrations, but not in the others studied, namely, 0.030, 0.100, or 0.140. They were found in all pH concentrations except 4.0, 9.0, 9.5, 11.0, and 11.5. This indicates that curved hairs are not common in alkaline solutions or solutions of higher concentration.

A type of abnormality which occurred in calcium chloride, but which in the report of the work on that compound (VI) was included under *curved*, has here been considered separately, and is given the name *sickle* (fig. 1, *9*). It consists of a combination of swollen and curved types, that is, the tip enlarged upon

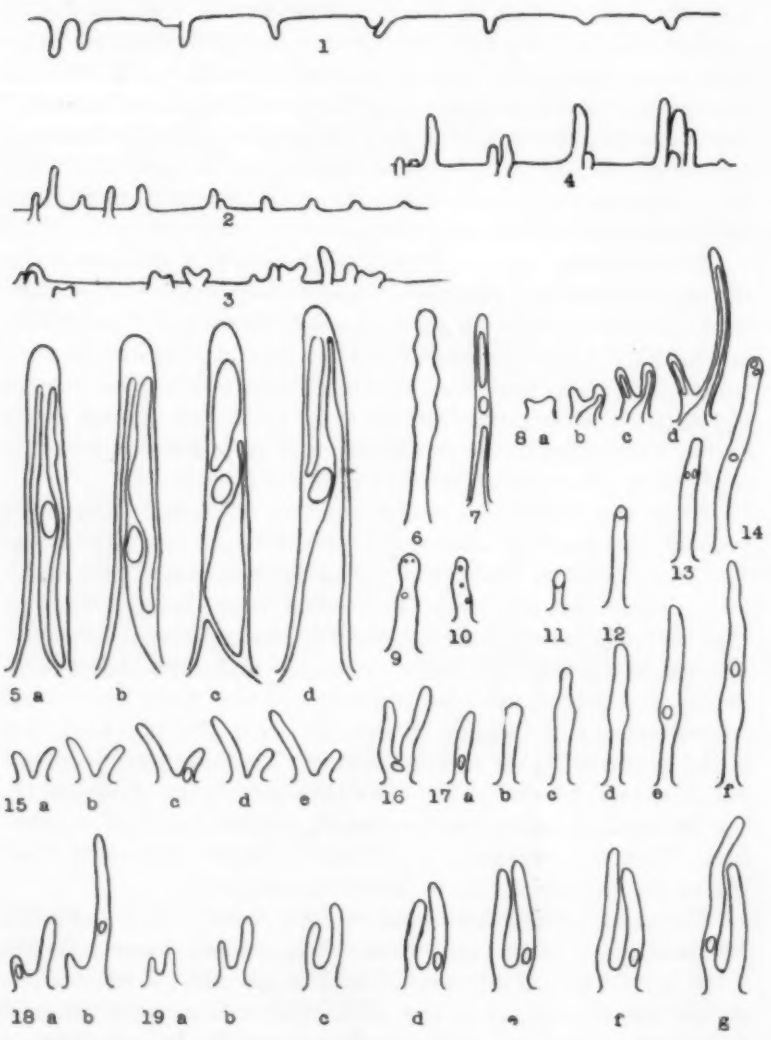


Fig. 2. Aquatic root hairs of collards in calcium nitrate. *1.* Eleven hairs showing spacing in 0.060 M. at pH 7.0. *2.* Eleven hairs showing spacing in 0.060 M. at pH 4.5. *3.* Eleven hairs showing spacing in 0.060 M. at pH 9.0. *4.* Eleven hairs showing spacing in 0.004 M. at pH 7.5. **5.** Vacuolar changes in a hair in 0.020 M. at pH 10.0, drawn at two minute intervals. *6.* Beaded hair in 0.008 at pH 10.0. *7.* Typical vacuolar and nuclear arrangements, 0.020 at pH 10.0. *8.* A duplex hair showing vacuoles in 0.020 at pH 7.0. The intervals are 30–30–150 minutes. *9.* Beaded hair in 0.012 at pH 11.0 with glistening bodies. *10.* Crooked hair in 0.012 at pH 11.0 with

immersion, and later growth was resumed at the same diameter, but in a progressively varying direction. This was found in 0.004, 0.008, 0.020, 0.030, and 0.060, and in all pH values except 4.0, 4.5, 7.5, 11.0 and 11.5. It, therefore, like the curved type is not found in concentrated solutions or in alkaline solutions, and in addition is absent from very acid media.

Branched amphibious root hairs (fig. 1, *3*, *4*, *7*, *13*,) were found in 0.004, 0.008, 0.012, and 0.020 M, but not in more concentrated solutions. They were not found in pH values below 6, nor in those of 7.5, 9.5, or 11.5. This means that they are characteristic of low salt concentration, and neutral or low hydrogen-ion concentration.

Another type of hair, is referred to here as *kinked* (fig. 1, *8*). It is a hair which does not enlarge at the tip upon immersion, but which resumes growth at the same diameter and in the same direction, but on a slightly different axis. It is found only in 0.008 and 0.012 M, and in pH 4.5, 6.0, 7.0, 8.0, 10.0, and 10.5. It therefore seems to occur only in moderately low salt concentrations, but in almost any hydrogen-ion concentration.

Spatulate hairs (fig. 1, *5*) were found in 0.008 and 0.012 M, and in pH 4.5 and 6.0. They likewise seem characteristic of moderately low salt solution, but are found only on the acid side.

Capitate hairs (fig. 1, *12*) on the other hand, are found in medium salt concentrations, and in acid, neutral, and slightly alkaline media. They were seen in 0.008, 0.020, 0.030, and 0.060 M, and in pH 4.5, 6.0, 7.0, 8.0, and 9.0.

Flask-shaped amphibious hairs (fig. 1, *6*) occurred in 0.012 M at pH 6.0 and 7.0. They are to be regarded as not fundamentally different from the capitate and spatulate types.

Crooked hairs (fig. 1, *10* and *11*) were found in 0.004 and 0.008 in pH 4.5 and 5.0. They therefore seem to represent the toxicity of acid solutions of low salt concentration.

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glistening bodies. *11–14*. Hairs in 0.004 at pH 11.5 with glistening bodies *15*. Duplex hair in 0.012 at pH 9.0. Intervals, 60–30–30–60 minutes. *16* Duplex hair in 0.008 at pH 10.5. *17*. Hair in 0.008 at pH 10.0. Intervals: 30 minutes. *18*. Duplex hair in 0.020 M. at pH 7.0. Intervals: 3 hours. *19*. Duplex hair in 0.008 M. at pH 9.0. Intervals: 30 minutes.

A new type of hair, not seen in calcium chloride or hydroxide, is called *beaded* (fig. 2, *6*). It was found in very alkaline solutions, pH 11.0, of 0.004 and 0.030 molar solutions. It is not a common type in these solutions.

Sloped hairs are such as take a direction at an oblique angle from the horizon of the root. They were seen in 0.012, and 0.030 M solutions of pH 10.0 and 10.5. They therefore are a

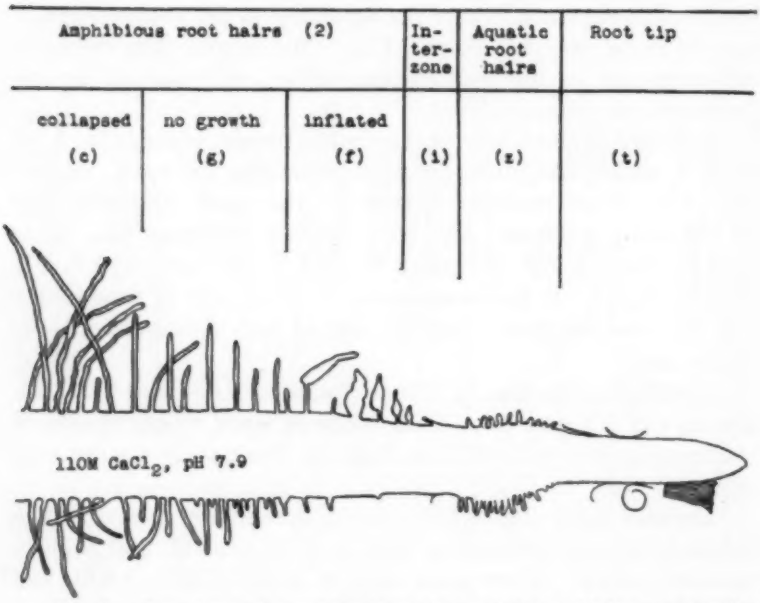

Fig. 3. Zonation and modifications of root hairs at high concentration of calcium chloride.

response to medium salt concentrations which are very alkaline.

In considering then the effect of immersing the roots of collards in calcium nitrate solution upon root hairs already growing, it must be concluded that the most common effect is either cessation of growth or growth, at least temporarily, at an increased diameter. This latter may give us any one of the following types, according to the type of subsequent growth: inflated, swollen, sickle, branched, spatulate, capitate, flasked, crooked, or beaded. Instead of this they may, in quite alkaline

solutions of medium concentration, become sloped or in low concentrations become kinked or, in acid or neutral solutions of low or medium concentration they may become curved. These three types may all be looked upon as a disturbance of the direction of growth. Such a disturbance is also seen in the later development of crooked, sickle, and undulating, all three of which are also characteristic of low or medium solutions, especially if they are acid. We may therefore conclude that a disturbance in the diameter of the root hair is a response to the shock of immersion in any solution, and that a disturbance of the direction of growth is an effect, immediate or subsequent, of immersion in a low or medium concentration. In low concentrations also we may have the original diameter resumed, as in the branched, beaded, and swollen. But in all solutions growth may continue, if at all, at the new enlarged diameter, giving the inflated type, which is the only one found in very high molar solutions.

INTRACELLULAR FEATURES OF AMPHIBIOUS HAIRS

Some intracellular features of amphibious root hairs were noted in addition to the form changes. In some solutions, amphibious root hairs were observed to have burst (table 25, *bur.*). These were in acid and alkaline solutions of moderate concentrations. Coagulated (*coa*) protoplasm was observed in hairs in very acid or very alkaline solutions or even in neutral solutions of low and moderately low concentrations. The evidence here would indicate that concentration of the salt rather than pH may be the more important factor in coagulation of protoplasm of hairs already well developed before immersion. Miss Addoms (133) finds coagulation especially characteristic of root hairs in very acid solutions, pH 4.0 or below.

A feature of amphibious root hairs, characteristic entirely of alkaline solutions, was the presence of glistening bodies. In some cases these had the form of isolated particles in the interior of the cell (fig. 2, *9*, *10*, *13*, *14*), and in other cases the entire tip glistened brightly (fig. 2, *11*, *12*). They were found in solutions of a pH of 9.0, 10.0, 10.5, 11.0, and 11.5, that is in all solutions more alkaline than 8.0, except 9.5. In the last named solution they may have been overlooked. They occur in

molar concentrations of 0.004, 0.008, 0.012, 0.020, and 0.030. They are therefore apparently prevented from forming by high concentrations of the salt.

FORMS OF AQUATIC ROOT HAIRS

Aquatic root hairs showed more abnormalities in calcium nitrate than in calcium chloride. The most common of these was the form known as *duplex*. It is similar to the branched, but we have applied that name only to the amphibious hairs which fork after growing for a time as a single hair. The duplex aquatic hairs, consist of two hairs arising immediately from a common base, and hence from a single superficial cell of the root. How commonly they may occur upon a single root is shown in figure 2, *3*. They were found in all concentrations up to 0.100, and in nearly all pH values 4.5 to 11.0. They occurred most commonly in moderate concentrations, 0.012, 0.020, and 0.030, and in neutral to moderately alkaline media, pH 6.0 to 9.0. A description of the vascuolar and nuclear movements within these duplex hairs is given below.

Crooked aquatic root hairs occurred in low concentrations, 0.004 and 0.008, and in high concentrations, 0.060, 0.100, and 0.140. They seem to be very little related to the hydrogen-ion concentration of the solution, being found in pH 4.5, 5.0, 7.0, and 10.5.

Inflated aquatic root hairs were seen in 0.100 M at pH 8.0 and 10.5. They may therefore be regarded as a response to alkaline solutions of high concentrations.

Capitate aquatic root hairs were found in 0.004, 0.008, 0.012, and 0.030, at pH 7.0, 9.0, 9.5, 10.0 10.5, and 11.0. They are therefore to be associated with alkaline solutions of low or moderate concentration. It is to be noted that the capitate amphibious hairs were most commonly found, on the other hand, in acid solutions.

Kinked aquatic root hairs occurred in 0.004, 0.008, and 0.012 M at pH 5.0, 6.0 and 9.0. This is quite the same type of solutions in which they were found among the amphibious hairs.

Beaded aquatic root hairs were found in 0.004, 0.008, 0.012, and 0.030 M. at pH 10.0, 10.5, and 11.0. This is much the same occurrence as have the beaded amphibious hairs.

Sloped aquatic root hairs appeared in 0.004, and 0.008 M.

at pH 10.5, and 11.5. It was noted above that sloped amphibious hairs were also to be found in very alkaline solutions.

TABLE 26

Forms of aquatic root hairs of collards in calcium nitrate

(*a*) *Hydrogen-ion concentrations*

pH	n	cap	dup	cro	kin	bea	cur	inf	slo	und	Total
4.0	+										1
4.5	+		+	+			+			+	5
5.0	+		+	+	+						4
6.0	+		+		+					+	4
7.0	+	+	+	+							4
7.5	+		+								2
8.0	+		+					+			3
9.0	+	+	+		+						4
9.5	+	+									2
10.0	+	+				+	+				4
10.5	+	+	+	+		+		+	+		7
11.0	+	+	+	+		+	+				6
11.5	+								+		2
	—	—	—	—	—	—	—	—	—	—	
FpH	13	6	9	5	3	3	3	3	2	2	

(*b*) *Molecular concentrations*

M	n	cap	dup	cro	kin	bea	cur	inf	slo	und	Total
0.004	+	+	+	+	+	+	+		+		8
0.008	+	+	+	+	+	+	+		+	+	9
0.012	+	+	+	+	+	+					6
0.020	+		+								2
0.030	+	+	+			+					4
0.060	+		+	+							3
0.100	+			+				+			3
0.140	+			+							2
	—	—	—	—	—	—	—	—	—	—	
F M	8	4	6	6	3	4	2	1	2	1	

For key to symbols, see table 25.

Numbers in the last column refer to number of types of abnormalities and the normal type found in each solution respectively. Numbers in the other columns refer to number of roots upon which normal hairs were found in the respective solutions.

Curved aquatic root hairs were recorded in 0.004, and 0.008 M. at pH 4.5, 10.0 and 11.0. They are therefore found in low concentrations of very acid or alkaline reaction. The range of curved amphibious hairs was greater, but in that case also none

was found in very high concentrations, and they were fewer in the neutral solutions.

Undulating aquatic root hairs were found in 0.008 M. at pH 4.5 and 6.0. They were therefore to be regarded as of rare occurrence as compared with their great frequency among amphibious hairs.

It is to be noted that there were many more abnormal root hairs of the amphibious type than of the aquatic. In many, if not most, cases only one root of the six observed in a given solution, showed hairs of the abnormal type noted. The number of roots with a given abnormality found in each concentration is indicated in table 26.

It is also to be noted that not all of the types of abnormalities noted among amphibious hairs were also found among the aquatic. Those which did not occur among the latter root hairs were: *swollen*, *sickle*, *spatulate* and *flask-shaped*. There were also no instances of *burst* or *coagulated* aquatic hairs observed.

In general the solutions having the most abnormal amphibious hairs also were most likely to have abnormal aquatic hairs. These were the low molar concentrations of 0.004, 0.008, and 0.012, and the hydrogen-ion concentrations near the limits of the range, that is, 4.5, and 10.5. This means that very acid and very alkaline hypotonic solutions give the greatest diversity of morphogenetic effects.

In comparing the abnormalities of amphibious and aquatic root hairs in calcium nitrate, it is to be noted that while they are of common occurrence among amphibious hairs, they are to be considered as rather rare among aquatic hairs. Furthermore there is very little evidence that the aquatic hairs alter their diameter markedly after beginning to grow. They may grow at a diameter which is greater than normal, but they do not ordinarily enlarge markedly after starting nor do they reduce their diameter at a later time. Their abnormalities seem rather to be either a matter of starting and continuing to grow at an unusually large diameter, or of changing their direction of growth. This change of directing of growth is found in the crooked, kinked, sloped, undulating, and curved types. The abnormally large diameter is represented by the inflated and capitate types. The only exception to the above is the case of

the beaded, which does result from a repeated change in diameter.

In general there seem to be more abnormalities in the calcium nitrate than in the calcium chloride solutions. As already noted the duplex aquatic hairs were not found at all in chloride, nor were the beaded aquatic or beaded amphibious hairs. Branched hairs were rarely seen in chloride, while being very common in nitrate. Undulating amphibious and aquatic hairs were also not found in the chloride. It would thus seem that the morphogenetic toxicity of nitrate is greater than that of chloride.

VACUOLES

The most common arrangement of vacuoles in single aquatic root hairs which was found in the calcium nitrate solutions is that represented in figure 2, *7*. It consists of a terminal elongated vacuole, separated from an extension of the basal vacuole by a region of protoplasm, frequently containing the nucleus. The basal vacuole is evidently an extension of the vacuole of the cell proper, of which the root hair is an extension. This vacuolar arrangement was recorded as occurring in 0.020 M. at pH values of 4.5, 6.0, 8.0, and 10.0, and in 0.030 M. at pH values 7.0 and 9.0. The failure to record it at other concentrations is not to be taken as evidence of its absence in them, as no specific effort was made to determine its occurrence.

In some solutions it was noted that there were rather rapid changes in the vacuolar system. The four drawings indicated in figure 2 as *5a*, *b*, *c*, *d*, respectively, represent the same root hair at successive two-minute intervals. This hair was growing in 0.020 at pH 10.0. The first stage shows the two vacuoles elongated and lying side by side with the nucleus and ambient cytoplasm between them. The left-hand vacuole is an extension of the basal vacuole. Presently (*b*) the right-hand vacuole is seen to contract and withdraw from the base of the hair. This leads to a division of the left-hand vacuole into an apical and a basal portion. These two parts separate widely, the former moving to the apex of the hair and the latter withdrawing almost entirely into the cell proper. Meanwhile (*c*) the right-hand vacuole moves in a basal direction and enlarges mostly below the nucleus. It is now observed that the basal vacuole of the cell proper connects with the right-hand vacuole,

which in turn elongates terminally, and pushes up past the left-hand vacuole in the apex. The latter (*d*) now pushes down along the left-hand side of the nucleus, causing a resumption of the original vacuolar condition, except that now the right-hand vacuole constitutes an extension of the main vacuole, instead of the left-hand vacuole as originally was the case. Meanwhile it will be observed that the hair has elongated appreciably.

It is apparent that in some instances, at least, these rather rapid vacuolar changes accompany rapid growth. They may have some relation to furnishing the tip of the root hair with an adequate supply of building material. They are evidently accompanied in many cases by active streaming of the cytoplasm between the vacuoles.

That the vacuolar situation is related to root hair elongation, is evidenced by a study of the duplex hairs. In many cases it was observed that one of the two hairs of the pair contained a vacuole which was an extension of the vacuole of the cell proper. The other hair contained a vacuole which was not connected with that of the superficial cell of the root. Almost invariably, as far as noted, the hair which contained the extension of the vacuole of the cell proper grew more rapidly than the other. In some cases the other hair did not grow at all. In figure 2, *8a*, *b*, *c*, *d*, are shown successive stages of a duplex hair growing in 0.020 M. at pH 7.0, and drawn at successive intervals. The first three are drawn at 30 minute intervals, and the last after the lapse of 2½ hours. It is to be noted that while both hairs grew at first when there was no secondary vacuole in the left-hand hair, the latter stopped growing very soon after the formation of such a vacuole. It may also be noted that, if the cytoplasm circulates around the extension of the main vacuole, from right to left, it will surge up into the left-hand hair after it has passed through the right-hand hair, if no vacuole is present in the former. But after the formation of a secondary vacuole in the left-hand hair, and after it has elongated somewhat, there will probably be much less circulation of cytoplasm up into the tip of the left-hand hair, and hence less building material will be available. Thus it is seen that the existence of vacuoles in duplex hairs may alter the streaming of cytoplasm in such a way as to determine the rate of growth of the two parts. In fact it is not unlikely that

vacuolar relations are equally if not more important, than nuclear relations in this connection.

NUCLEUS

The nucleus was observed in many instances to be present in the root hair about 100 microns from the tip. This distance was, however, by no means constant. On the other hand many hairs of considerable length grew at a very rapid rate, without the appearance of the nucleus in the hair. No data as to the number of hairs containing and devoid of nuclei were recorded, but one gained the definite impression that there were approximately as many of the one as of the other.

Cases were noted of single hairs into which the nucleus moved from the cell proper, and then later migrated back, remaining there apparently permanently. In some instances, however, the nucleus was later observed to emerge again into the hair and to assume the characteristic position. Such relationship is shown in figure 2, *17*, *a*, *b*, *c*, *d*, *e*, *f*, which are of the same root hair grown in 0.008 M calcium nitrate at pH 10.0 drawn at successive thirty minute intervals. It is to be noted in this case, that after the withdrawal of the nucleus into the cell, the diameter of the tip of the hair increases somewhat, giving the hair an inflated appearance. When the nucleus at a somewhat later time returned into the hair, the hair resumed its original diameter for growth. Judging from this single instance, then, it might seem that the presence of the nucleus has something to do with the extent of the area of cell wall deposition at the tip of the hair. It may be that the origin of inflated, capitate, spatulate, swollen, and other abnormal types of hairs may eventually be related to the effect of the solution upon the migration of the nucleus. However, at present the only evidence in this direction is that which has just been presented in the drawing referred to above.

Some evidence may be secured as to the relation of the position of the nucleus to root hair growth by a study of the duplex hairs. In some instances (fig. 2, *16*) the nucleus takes a position at the region of juncture of the two hairs of the pair. In this case the two hairs are observed to grow at approximately the same rate. However, so few hairs of this type have been seen, that generalization on the relation of the central

position of the nucleus to the growth rates of the two hairs is not warranted as yet.

It was observed in some instances that the nucleus may move into one of the hairs and then retreat again to the cell proper. Such movements seem to have no relation to the rates of growth of the respective hairs. In the instance illustrated (fig. 2, *15, a, b, c, d, e*) there are shown five drawings of the same hair at 45 minute intervals, growing in 0.012 M at pH 9.0. At first the right hair is longer, then the left hair gains the ascendency. Soon thereafter the nucleus emerges from the cell proper into the hair which is growing more slowly, or which, in fact, has ceased growing. Later it retreats to the cell proper, and remains there to the close of the period of observation. On the basis of observations reported below, it might be expected that the nucleus would later emerge in the hair which was growing at a normal rate. The solution in which this duplex hair was growing was 0.020 M at pH 7.0.

Several instances were found in which the nucleus migrated from one of the twin hairs to the other. In one such case (fig. 2, *18a, b,*) the nucleus moved into a hair which had ceased growing or, at least, did not grow appreciably thereafter, and then migrated over to the other hair which was growing at a normal rate. The time interval between the two sketches in this case was three hours; and the solution was 0.020 M at pH 7.0.

Another duplex hair was studied more intensively in this regard. At first both hairs grew at about the same rate, the right a little faster. Into this hair the nucleus emerged from the cell proper. Almost immediately the other hair began growing faster, and finally equalled and exceeded the right hair in length. A short time after this had happened, the nucleus was observed to move around into the hair which now was growing the more rapidly (fig. 2, *19 a, b, c, d, e, f, g*). Drawings made at 30 minute intervals are shown of these stages of growth and nuclear migration. The root was growing in a solution of 0.008 M at pH 9.0.

From the data here presented it might be suggested that the nucleus may have some inhibitory effect upon the elongation of the hair in which it is located. Three instances are shown and drawn in which the hair of the duplex into which the nucleus moved ceased growing almost immediately thereafter.

That such an inhibitory effect is chemical can hardly be assumed, because of the common occurrence of nuclei in single root hairs which grow normally. It is, however, conceivable that the nucleus may retard and even stop growth in one of a pair of duplex hairs, due simply to mechanical obstruction of the streaming protoplasm. It is obvious that the rapid elongation of the root hair must mean a very rapid transport of cell wall building material, especially the carbohydrates, like the pectic bodies, to the tip of the root hair where they are deposited. Any obstruction to such transport, it would seem, will most certainly retard elongation. In the case of the duplex hairs, such an obstruction may result in the diversion of the streaming almost entirely to the other hair, resulting in complete cessation of growth in the hair in which the obstruction lies. This seems to be the relationship of the nucleus to these hairs which cease elongating. In the case of single hairs, it has been shown (fig. 2, *17*) that the withdrawal of the nucleus may result in a growth at a broader diameter. It is conceivable that the removal of the obstruction may have allowed a sudden influx of material, which was then deposited simultaneously over a larger area, rather than held in reserve for deposition at a slightly increased rate over the same area.

The explanation of the migration of the nucleus from the hair which has ceased growing or is growing much more slowly, is, however, not quite so apparent. It has been assumed that the nucleus in one hair obstructs the protoplasmic streaming in that hair, while it goes on rapidly in the other. Unfortunately the hairs of *Brassica oleracea* are not suited for the study of protoplasmic streaming, because of their small diameter, and the absence of particles in the protoplasm. It is to be hoped that some plant which shows streaming in the root hairs more favorably will be found, which will also produce duplex hairs in these solutions. From the data at hand, however, it seems that the nucleus tends to move, whether passively or not, toward the region of greater activity. This activity consists in more rapid growth rate, and doubtless also more rapid cytoplasmic streaming.

As has already been noted, Haberlandt (7) and his student, Windel (39) have concluded that the position of the nucleus in the hair is to be taken as evidence that the nucleus is an active

factor in the growth of the root hair. The evidence here presented from a study of these duplex hairs, on the other hand, indicates that such a conclusion is not justified. The root hair apparently does not grow rapidly because of the presence of the nucleus; but it seems rather to be true that the nucleus may be present because the root hair is growing rapidly. As was shown above (fig. 2, *8*) it is likely that the vacuoles play a more important part in determining the growth of the root hair than does the nucleus. It seems, in fact, that the presence of the nucleus in the hair, instead of stimulating its elongation, may act as a retardant, by constituting an obstruction to the free flow of materials.

DISCUSSION

The migrations of the nucleus into and out of single and duplex hairs, and from one hair of a pair to another, and the more or less rapid change in the form, size, and connections of the vacuoles, together with the protoplasmic streaming which has been observed in root hairs of numerous species, and is especially prominent in aquatics such as *Hydrocharis*, *Trianea*, *Limnobium*, all point to the conclusion that the growing root hair is the seat of very active intracellular phenomena. The changes in form of the root hairs, which consist in changes in diameter at the tip, or changes in direction of growth of the tip, together with the observations of others, especially Ziegenspek (41, 42) as to the difference in chemical composition of the tip, all indicate that the growth of the hair takes place by the deposition of wall material over a restricted area at the very tip. In the simple salt solutions which have thus far been used in these experiments, very little material for wall formation enters from the outside. In the solution used in the present study there is only water and calcium nitrate. Of this latter material the calcium is probably the only constituent which is used in wall formation. The work of Miss Howe (12) has shown that the cell wall consists of callose and calcium pectate. Ziegenspek finds that the tip is largely if not entirely amyloid. It would seem then that the substance of which the new primary wall is constructed at the tip of the hair is of internal origin, arising in this case from the carbohydrates stored in the seed, and transported to the root hairs of the young seedling. There must be therefore a constant and very rapid transport of carbo-

hydrate into the root hair to enable it to grow at a rate of as much as 100 microns or more an hour. Any obstacle like a nucleus or a vacuole is likely to retard elongation, unless it is so placed as to divert the streams of protoplasm toward the tip, rather than to form eddies and return them to the cell proper without reaching the tip.

But this transport of carbohydrate to the tip is not the only type of conduction involved in the root hair. The calcium enters presumbably along the lateral sides of the root hair and also perhaps at the tip. It is partly or largely deposited as calcium pectate, either through alteration of the amyloid as a source of carbohydrate, or, what is more likely, by an exchange with potassium of potassium pectate in the cell sap. In the latter case there would then be a transportation of potassium pectate into the root hair as well. We thus have the movement of calcium and of carbohydrate for secondary wall formation.

There is furthermore additional movement of inorganic ions. Carbon dioxide is formed in all of the cells of the seedling root and is carried out from cell to cell to the surface. Inasmuch as the surface of the root hairs is as great or greater than that of the remainder of the root, much of this carbon dioxide will find its way into the root hair before being liberated into the solution. Some of this carbon dioxide will be given off in exchange for nitrate ions. In alkaline solutions, especially, it is likely to be given off in exchange for hydroxyl ions. Inasmuch as so much calcium is used in the root hair, and inasmuch as calcium is the only element absolutely necessary for their growth it might be concluded that more calcium would be absorbed than nitrate. However, Hoagland and Davis (110) working with barley, and Hibbard (108) working with wheat, find that from calcium nitrate solutions more nitrate is abosrbed than calcium. This is, however, probably to be interpreted not as evidence of a greater utilization of the nitrate in the root hair, but of a greater permeability of the membrane to nitrate ions. This may, in fact, be due to a greater supply of anions, especially CO_2 to exchange for the nitrate, than there are of cations, especially K, to exchange for the calcium.

We are thus to picture an exchange of ions at the surface of the root, the cation, Ca, going in, and the cations, K and H, coming out in exchange; the anions NO_3 and OH going in, and

the anion CO_2 coming out. Whether or not the H ion passes into the root, even from acid solutions, may be open to question. There is always carbon dioxide coming out, and it is conceivable that these CO_2 ions may come from inside to the surface of the root hair accompanied by K ions, which, however, do not pass out of the root hair, but are exchanged at the surface for the H ions already present in the solution. It is also doubtful if OH ions pass out into the solution from the hairs, inasmuch as the other anion, CO_2, is probably always present in sufficient amount.

To complete the picture we must think of the potassium ions as accompanying the nitrate ions on their journey into the root proper from the root hair. These potassium ions came originally from their storage place in the seed. They have passed into the root hair in company with organic anions such as pectate and oxalate, and also perhaps with the inorganic anion, CO_2. Here at the cell wall or on the cell interior they are exchanged for calcium or perhaps hydrogen ions, being themselves left in the root hair, to travel back into the root with NO_3 or OH ions. It has already been pointed out (VII) that the root responds differently to various hydrogen ion concentrations of calcium hydroxide solutions than does the root hair. This was explained on the basis of the deposition of the calcium in cell wall formation of the root hair, and the penetration of the hydroxyl ion into the region of cell elongation of the root proper.

Popesco (183) has published a long paper in which he presents much data, and arrives at the conclusion that the region of absorption of the root varies somewhat in different plants, but that it usually embraces the hairless portion below the region of root hairs, as far as the meristem, and also the region of youngest root hairs. He decides that the root hairs rapidly lose their ability to absorb, and become an impervious tissue. Even if his conclusions are fully accepted, there would be no doubt but that the aquatic root hairs up to the age studied in this series of papers, that is, three to five hours, would be absorbing organs. However it is not quite certain that his conclusions should be accepted without critical examination. It will be observed that he grew the root hairs in air, then immersed the root, and studied the same root hairs after immersion. His data are then based entirely upon amphibious root

hairs. We have shown that these amphibious hairs do not usually behave normally. Their protoplasm may coagulate, they may cease growing, without visible evidence of injury, or they may take on bizarre types of growth. The failure of these hairs to absorb dyes, therefore, does not necessarily demonstrate that they are normally impervious structures. Furthermore the absence of absorbed dye, even if the hairs were normal, would not mean that they did not absorb water or even inorganic mineral ions.

Strugger (201) has recently published an extensive study of vacuolar conditions and streaming in root hairs of barley in different hydrogen ion concentrations. His method consisted of cutting off the root and mounting it on a slide in a sodium acetate buffer solution. In view of the evidence obtained by others as to streaming as a traumatic response, the question may be raised as to the validity of this evidence as reflecting the normal condition in these root hairs. He studies these root hairs in a range of hydrogen ion concentrations which seem to us exceedingly narrow, pH 5.60 to 6.80. The normal condition he defines as the same situation as we have above refered to as normal (fig. 2, 7). This condition he finds at 6.80 to 6.40, and at 6.10 to 5.90. At hydrogen ion concentrations just above (lower pH) each of these ranges he finds no apical vacuole, and at a little higher concentration still in each case, numerous small vacuoles. He regards pH 5.6 as the lethal boundary. He thus obtains a bimodal curve for vacuolar condition, and also finds a similar curve for streaming, although he presents no tables of data or percentages of instances. He attempts to interpret these bimodal curves on the assumption that the isoelectric point of the nucleus is 6.35 and that of the cytoplasm is at 6.15. But he comes to the conclusion that this interpretation will not hold, inasmuch as the results are different under different conditions.

In two recent papers reviewing the cancer problem, Sokoloff (202, 203) comes to the conclusion that

> The cellular anarchy, which is connected with the biological process of the rejuvenescence of cells, has its origin in the alterations of the cellular membrane and of the cellular lipoids. The nuclear alterations, which have been observed in the cancerous cells are secondary phenomena, resulting from the breaking of the lipoid equilibrium in the tissues.

In view of this conclusion it is interesting to note the present tendency to avoid attempting to relegate all forms of cellular activity to nuclear influence, and to explain the behavior of the nucleus, in part at least, as the result of external influence upon it. In our interpretation of the growth and behavior of root hairs, and the intracellular phenomena associated with them, we have endeavored to reduce it to a physico-chemical basis, as far as possible, correlating it with cell wall activity, rather than attributing it to a deep seated nuclear influence.

Biological thought a century ago was concerned very much with the consideration of the usefulness or the uselessness of organs or functions. It was considered that the organism responds to a change of the environment by becoming modified in such a way as to be fitted to live under the new conditions better than if it had remained unchanged. This concept was included in the term, adaptation, and played a very important part in the contributions of Lamarck and Charles Darwin and their contemporaries. More recently the modifications brought about by changed environment have been interpreted rather from the physico-chemical standpoint, their usefulness or uselessness being regarded rather as incidental or accidental. Recent biologic literature is replete with studies on the so-called toxicity of chemical entities, and with the modifying effects of light, temperature, electricity and various types of radiations. The question has been brought forcefully to the popular mind, through the evidence of shock occurring in war, and the resultant rapid or slow recovery or permanent injury. This medical aspect of the problem has largely been related to the changes occurring in the nervous system of human beings. The phenomenon of shock and recovery can, however, be shown to exist in all quite different types of cells as well, and may be regarded as a fundamental cellular property. It is, in fact, well demonstrated in its structural aspect, at least, in these amphibious root hairs described above.

There is, in some instances, serious injury, resulting in death of the cell. This may be so extreme as to consist of bursting or coagulation of the protoplasm. In other less severe cases, the constitution of the protoplasm remains unchanged apparently; but the hairs cease growing. At the other extreme there are those very young amphibious hairs which show no

structural or functional modification at all. It has been shown (V, text fig. 11) that this occurs only in solutions supporting an optimum growth rate. In other solutions the least injured hairs show no structural modifications, but they do cease growing for two to four hours, and then resume it at the original diameter and direction. This is in fact the minimum exhibition of shock and recovery. The next type in order is the so-called *swollen* amphibious root hair, in which there is a temporary modification of diameter, followed by a resumption of growth at the original width. Here with a minimum structural demonstration the kinked hair would be coordinate with the swollen in this respect of shock and rapid recovery. The *branched* type, however, shows almost as little injury. The effect is temporary, but there is a permanent modification, due to a subdivision of the growing zone. In the *flask*-shaped hair, there is an instance of shock and gradual recovery. The *inflated* and the *capitate* hairs show permanent unchanging injury; while the *spatulate* hair constitutes a case of accelerating injury with time, inasmuch as it is progressively getting broader and broader. Other instances of this same sort of reaction are found in the *curved* and *sickle*, in which the shock is followed by a progressive change in direction. Then there are cases in which the shock has set up a rhythmical periodicity in which there is a recurrence of the new condition alternating with a return to the original; such are the *undulating* and *beaded* types of amphibious hairs. The most severe injury exhibited morphologically, and standing next in order to the type which does not grow at all, though appearing unchanged, is the *crooked* type, which has apparently lost all sense of conformity to a system of growth. It is undoubtedly a far cry to attempt to correlate these cellular reactions with the psychological and physiological cases of shell shock. And yet there seems to be a parallelism, which serves to emphasize the fundamental nature of protoplasm, and the unity of life as it occurs on the earth.

SUMMARY VIII

73. In neutral and acid solutions of high salt concentration there is a tendency toward equidistant spacing of the aquatic root hairs. In alkaline solutions and in solutions of low salt

concentration there is a tendency toward clustering of these root hairs.

74. Amphibious root hairs are found to respond in various ways to transfer to the solution. The differences in these responses are attributable in part to the composition of the solution, in part to the age of the hair, and in part to the individual differences between the hairs. The series of modifications in order from most severe to least effect is as follows: bursting, coagulating, no growth without visible alteration, crooked, sickle, curved, spatulate, beaded, undulating, inflated, flask-shaped, branched, kinked, swollen, temporary cessation of growth without visible alteration, temporary retardation of growth rate, without visible alteration, no alteration of growth rate of structure. This series may be correlated with types of shock and recovery.

75. Aquatic root hairs do not display so many types as do the amphibious. There are: crooked, inflated, capitate, curved, undulating, beaded, sloped, kinked, and duplex. Of these the last-named was the most common type. More abnormalities occur in the calcium nitrate than in calcium chloride.

76. The usual vacuolar arrangment consists in one terminal elongated vacuole, and a basal vacuole, which consists of an extension of the vacuole of the cell proper. In some instances rapid changes in form, size, and division and fusion of these vacuoles were seen to take place. Some evidence was obtained especially from a study of duplex hairs, which indicates that the vacuolar complex may effect the rate of root hair elongation, by determining the freedom of flow of building materials to the tip of the root hair.

77. The nucleus most commonly lies in the protoplasm between the two vacuoles and moves along at a rather constant distance behind the tip. It is however not present in many hairs which appear to grow normally. It may enter a hair and then retreat to the cell proper again, or it may move from one hair of a duplex which is not growing well into the other which is already growing more rapidly. It is concluded therefore that the nucleus tends to move toward the region of most rapid growth; but it is thought that the nucleus does not cause the rapid growth, but rather that its presence may bring about retardation, due to interference with lines of flow of cytoplasm.

78. The paths of movement of organic and inorganic ions during the growth of root hairs in such a solution as calcium nitrate are discussed, and correlated with the observations so far made.

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A CORRECTION

A misstatement in no. VII of this series of Studies (Bull. Torrey Club **55**: 238. May 1928) should be corrected:

The culture solutions described in paragraph 2 (page 238) were prepared from a 0.0114 M stock solution of calcium oxide (rather than from a saturated solution of calcium hydroxide) by the addition of 1.0, 1.25, 1.5, 1.75, 2.0, and 4.75 cc. each to one liter of distilled water, so that the resulting molar concentrations were: 110^{-7}, 140^{-7}, 179^{-7}, 200^{-7}, 230^{-7}, and 540^{-7}.

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